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PART I.—GENERAL

CHAPTER I

EXTERNAL MORPHOLOGY AND PHYSIOLOGY

1. Unicellular and Multicellular Plants

The lowest plants are of microscopic size and have a relatively simple structure. For example, the green, powdery deposit often seen on the bark of trees or the surface of old wooden palings usually consists of a minute Alga named *Pleurococcus*. Viewed under the microscope, each individual (Fig. 1) appears as a rounded sac consisting of a cell-wall enclosing the living protoplasm in which can be distinguished a lobed, green body containing the green colouring matter called chlorophyll, and a spherical, dense, colourless body in the centre, the nucleus. Such a structure is called a cell. The lowest forms of plant-life are one-celled or unicellular. In all the highest forms the plant-body is multicellular, *i.e.* it consists of numbers of cells aggregated together and closely united with each other.

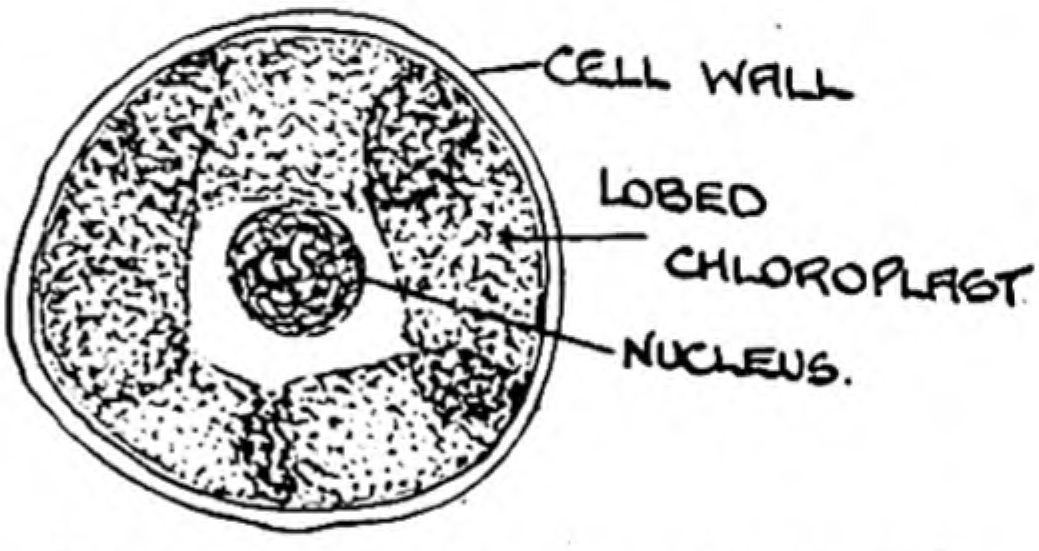


Fig. 1. *Pleurococcus*. A Unicellular Alga.

2. Differentiation

In unicellular plants all the vital functions are carried on by the single cell; but in multicellular forms, as a rule, different parts of the organism take on different functions; each part has a form and structure related to the performance of its particular function, and is said to be specialised. Thus the organism consists of parts differing from each other. Seeing that these various functions are carried on for the good of the organism as a whole, it is evident that in such an organism there is **Division of Labour.** The distribution of functions which characterises this division of labour is called **Physiological Differentiation**; and the marking off of distinct parts serving as the organs of particular functions, which is correlated with it, constitutes **Morphological Differentiation.**

It is evident that morphological and physiological differentiation go hand in hand. In the lower forms there is comparatively little division of labour, and morphological differentiation is only slightly marked. As we ascend from lower to higher forms, however, we find that the arrangements become more and more numerous and complex, and the division of labour correspondingly extensive. Hence it is in the highest plants that we meet with the most pronounced and far-reaching differentiation of organs. In fact, we tend to distinguish between lower and higher forms by the degree of differentiation and division of labour exhibited in each case.

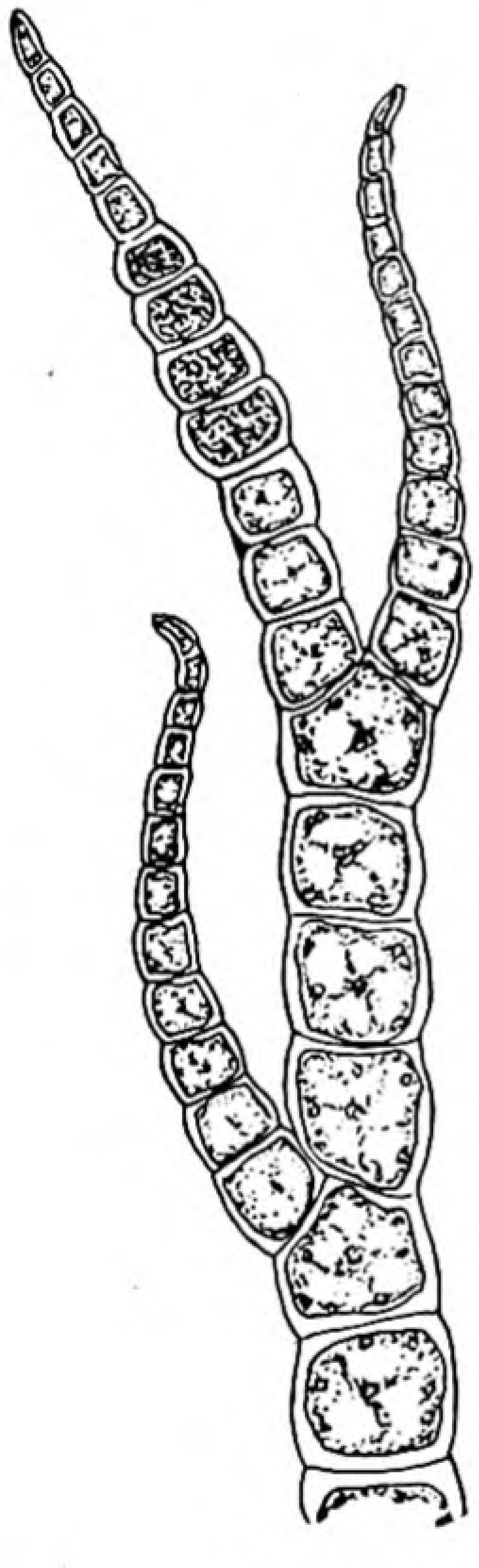


Fig. 2. *Pilayella.* A BRANCHED FILAMENTOUS ALGA.

3. The Thallus

Amongst the Thallophyta (p. 4) the plant-body is often very simple. It may be unicellular; when multicellular, it may consist of a flattened membranous expansion, or of a mass of branched or unbranched filaments which are all alike (Fig. 2). In some higher forms of Thallophyta, however, we find a differentiation somewhat resembling that into stem and leaf organs seen in the shoot of Seed Plants. A vegetative plant-body which is undifferentiated, or only slightly so, is called a **thallus.** It is specially characteristic of the Algae and Fungi, although not confined to these; hence the name Thallophyta for the division in which they are placed by systematists.

4. Shoot and Root

In many liverworts (e.g. *Pellia*) the plant-body is a thallus, but in the so-called leafy liverworts there is some differentiation into stem- and leaf-like parts. In the mosses this differentiation is more complete, but in none of the Bryophyta is there a true root; during active vegetative growth the entire plant is usually in intimate contact with moisture.

The differentiation of root and shoot is seen in Pteridophyta and Spermatophyta, and is related to terrestrial conditions of life. The root generally grows downwards; it branches repeatedly in the soil, the branches are similar, serve to fix the plant in the soil and absorb water and mineral salts.

The shoot tends to grow upwards towards the light. It consists essentially of two kinds of organs, **stems** and **leaves,** and is concerned with nutrition and reproduction. In many Pteridophytes there is only one kind of shoot, whose leaves perform both vegetative and reproductive functions; but in others there is a differentiation of two kinds of shoot, one purely vegetative, the other reproductive. This differentiation is carried still further in the Seed Plants, where reproductive shoots (floral region) are clearly marked off from vegetative shoots (foliage region). The flower may be regarded as a shoot whose leaves are specialised in relation to reproduction.

In the foliage region specialisation may also be found, in some cases so extreme that it is not easy to recognise a leaf or a stem as such. Roots also may be modified in relation to special functions.

Besides roots, stems and leaves, there may be outgrowths from any of these of the nature of appendages or emergences. These include various kinds of hairs, prickles, etc.

5. Branching

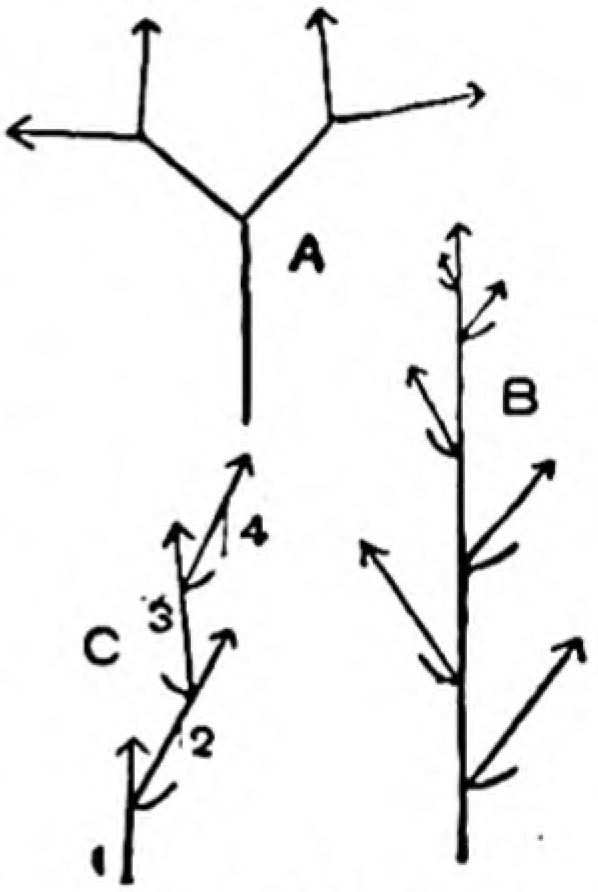


Fig. 3. Types of Branching.

A, Dichotomous;
B, Racemose (Monopodial);
C, Cymose (Sympodial).

When a main root branches it gives rise to secondary roots, *i.e.* similar parts. On the other hand stems may bear secondary stems and also leaves, *i.e.* both similar and dissimilar parts. The development of similar parts is called branching.

There are two chief types of branching —(*a*) dichotomous, and (*b*) lateral. In dichotomous branching (Fig. 3, A) the growing apex divides equally into two, and each part may become a branch. This branching thus consists of a series of bifurcations, but modifications may arise through the unequal growth of the branches or by the abortion of one of the growing points. True dichotomy probably does not occur in the Spermatophyta, but examples are found in Pteridophyta and Bryophyta, and are common amongst the Thallophyta. The branching of the thallus of *Fucus* is a good example of dichotomy. In lateral branching the branches arise as lateral or secondary outgrowths behind the growing point of the parent member or primary axis. This is the characteristic mode of branching in the Spermatophyta. If the primary axis continues to grow from the same growing point (*i.e.* is a monopodium), and also develops numerous lateral branches, one after another (in acropetal succession), the lateral branching is said to be indefinite or racemose (Fig. 3, B). If, however, the primary axis ceases to grow, e.g. by the death of its growing point at the end of a season, and growth is continued by one or more lateral branches (secondary axes) repeating the process, the branching is said to be definite or cymose, and the growth sympodial (Fig. 3, C).

6. Nutrition and Growth

We have already seen that the simplest forms of plant life are unicellular and that the cell consists of protoplasm, including a nucleus, and containing one or more chloroplasts enclosed in a delicate membrane—the cell-wall. The protoplasm is the living substance of the cell. The cell-wall supports and protects the protoplasm. Frequently the cell is not full of protoplasm. This may only form a lining to the inner surface of the cell-wall, and the central region of the cell, which is known as the vacuole, contains cell-sap—a watery solution in which may be dissolved various organic and inorganic substances.

If we observe such an organism carefully we find that it increases in size (grows) and multiplies (reproduces). It is evident that there must be some source from which it draws food-materials, and that the cell must possess the ability to build up these food-materials into its own substance. The processes involved in this are the same in kind as those carried on by all green plants. In unicellular plants they are, however, all performed by a single cell. The first consideration is that of food-materials, which, owing to the presence of a cell-wall, cannot enter the cell in solid form. They are absorbed from solutions. Here we have what is sometimes regarded as a fundamental difference between animals and plants. Animals can ingest solid food-material. Plants cannot do this.

Pleurococcus (§ 1) grows either in water or on some moist substratum, and the water, with various substances in solution, passes through the cell-wall by diffusion. When inside the cell certain of the dissolved substances may be absorbed by the protoplasm, and either be retained by it or passed into the central vacuole, if there is one in the cell. The dissolved substances are of a relatively simple character. The most important of them are certain mineral substances such as the nitrates, sulphates, and phosphates of various metals, and carbon dioxide (CO_2). Here we have another important point of distinction between animals and green plants. Green plants take in their food-material in the form of simple *inorganic* substances. Animals, although they need a supply of inorganic salts, must feed on complex organic substances such as fats and oils, carbohydrates (sugars and starch) and proteins.

7. Photosynthesis

The question now arises—how are these simple substances built up by the plant into living protoplasm? This is an organised but unstable complex mixture of proteins and fatty bodies containing nitrogen, sulphur, phosphorus, carbon, hydrogen and oxygen, but whose exact composition has not yet been determined, and whose properties are probably as much a consequence of its structure as its chemical composition. The building up of such a complex, unstable mixture from simple substances necessitates the expenditure of energy. In animals energy is derived from the complex organic food-materials which have been absorbed. The fats, proteins and carbohydrates which form the bulk of the food of an animal contain a large store of potential energy. The simple substances which form the food-materials of the green plant contain little or no potential energy. What then is the source of energy?

The answer to this question is to be found in the fact that the *green* plant possesses the ability to build up organic substances from inorganic compounds, using light as its source of energy. From water and carbon dioxide it is able to synthesise substances of the nature of carbohydrates, e.g. sugars. This process is known as carbon assimilation or *photosynthesis*, and is carried on only in the presence of light and chlorophyll. It is the chlorophyll that enables the radiant energy of the sun to be used in this particular way. When the simpler carbohydrates such as sugars have been synthesised, more complex substances such as cellulose, of which the cell-wall is composed, can be elaborated. Some of the carbohydrate is utilised together with absorbed nitrates for the synthesis of new proteins, the energy required for this process being derived from the oxidation of a part of the sugar formed during photosynthesis. A further portion of the carbohydrate present may undergo transformation into fats or oils, and finally, some of the complex substances formed may be utilised by the already existing protoplasm in building up more protoplasm. Both plants and animals build up new living protoplasm from complex compounds; but whereas animals obtain these already manufactured (by feeding on plants or other animals), green plants have to elaborate them from simple inorganic substances.

8. Respiration. Transpiration

The processes involved in the metabolism of all living organisms are especially interesting because of their energy relations, since energy is required for growth, and, indeed, for the maintenance of every living cell in a healthy condition; and since energy can be utilised only at the point where it is liberated, it follows that katabolic processes involving the release of energy must be occurring in every living cell. The sugars built up during photosynthesis represent a store of light energy which becomes available to the cell when these compounds are broken down by oxidation during the process of *respiration.*

We stated earlier that photosynthesis involves the building up of carbohydrates from carbon dioxide and water, and we can represent this process by a chemical equation:

$$6CO_2 + 6H_2O + \text{Energy} \xrightarrow[\text{of chlorophyll}]{\text{in the presence}} \underset{\text{glucose.}}{C_6H_{12}O_6} + 6O_2.$$

The reverse of this equation:

$$C_6H_{12}O_6 + 6O_2 \longrightarrow 6CO_2 + 6H_2O + \text{Energy}$$

similarly represents the process of respiration, although photosynthesis and respiration are much more complex processes than these equations indicate, each consisting, not of a single chemical reaction, but of a whole series of reactions.

There is evidence that it is mainly sugars that are oxidised during respiration, with the liberation of energy, although other substances such as fats and possibly proteins, and in some cases organic acids present in the cell, may be oxidised. The oxidation is not always complete. Instead of carbon dioxide and water being the sole products of the oxidation, simple organic substances may be formed, and some of these may be used again in nutrition (plastic substances), whilst others may be of the nature of secretions, or may be waste products of no further use to the plant.

These metabolic processes have been largely explained in terms of physics and chemistry; but the impossibility of carrying out under laboratory conditions many of the chemical reactions involved serves to emphasise the important part played by the living protoplasm in regulating and controlling them in the living organism.

Although we have described the general processes of metabolism with special reference to a unicellular plant, they hold good for all green plants. Thus a seaweed absorbs dissolved inorganic material over its whole surface, and, except in very large seaweeds, each cell is capable of absorbing food-material and of carrying on all the anabolic and katabolic processes exhibited by a unicellular plant. With increasing size and complexity of the plant-body we find, however, a specialisation both of form and of function. Food-materials synthesised in one part of the plant may be translocated to another part and there utilised. In the normal land-plant, for instance, the root not only fixes the plant in the soil but absorbs water and mineral salts. In root, stem and leaf a special system of conducting tissue is developed, and through this water and dissolved substances are conveyed to the aerial parts of the plant. Not all the cells of such a plant will contain chlorophyll. Usually only the leaves and younger parts of the stem are green, and it is these parts of the plant which absorb carbon dioxide from the atmosphere and, when exposed to light, synthesise carbohydrates from this carbon dioxide and the water supplied by the roots. The products of this photosynthesis are then distributed throughout the plant and used in the processes of growth, or in respiration, or stored for utilisation later.

Besides carrying on photosynthesis the leaves, in common with other living organs, respire actively, this process being unaffected by exposure to light. The leaves also give off large quantities of water vapour into the atmosphere in a process known as *transpiration*.

9. Food Storage

We have indicated above that not all of the food-materials synthesised by the living plant are used at once, but that some may be stored. Food substances are generally stored in insoluble forms such as starch and oil, but we sometimes find abundant stores of soluble food-materials, such as sugars. Often the food is stored in special parts or organs, e.g. bulbs, tubers, corms and seeds. From what we have said it will be clear that the green plant will not be able to grow for any extended period unless it is exposed to light so that it can carry on the process of photosynthesis. Bulbs, corms, etc., can often grow for a considerable time in the dark. They do this by virtue of the stored food substances that they contain. When this store of food has been exhausted they cease growth, unless they are exposed to light and thus able to build up new carbohydrates from simpler inorganic substances.

10. Enzyme Action and Translocation

When food-materials are stored in an insoluble form, they must be converted into soluble substances before they can be translocated in the plant. This conversion, in the plant, is effected by means of substances called enzymes, which we can for the moment define as organic, colloidal catalysts produced by the activity of the living protoplasm. There is evidence that the formation of insoluble substances from soluble ones, e.g. starch from sugar, is due to the same enzymes that effect their solution. With the help of the appropriate enzymes, chemical changes, which would otherwise proceed at a measurable rate only at high temperatures, take place at normal temperatures. For example, the conversion of starch to sugar (glucose), which can be brought about by boiling the starch with dilute acid, is effected with the help of the enzyme *diastase* at ordinary temperatures. There is increasing evidence that enzymes are important not only in effecting these conversions of insoluble substances to soluble ones and vice versa, but also in such important metabolic processes as photosynthesis and respiration.

11. Plants without Chlorophyll

Some plants have no chlorophyll, e.g. the Fungi (moulds and toadstools), Bacteria and a few flowering plants. It will be evident that these plants are incapable of synthesising organic substances from simple inorganic compounds. They resemble animals in that they must be supplied with complex organic materials. They may obtain these materials either from living organisms or from dead organic substances. In the former case they are **parasites,** and they may live on either other plants or animals (including man), and cause various diseases. They generally form special absorbing organs which obtain nutriment from the living cells of the host. When they live on dead organic material they are called **saprophytes,** and may be important agents in promoting the processes of decay.

12. Reproduction

The methods of reproduction met with in plants are commonly distinguished as **sexual** and **asexual.**

The *sexual* method involves the production of two sexual cells (**gametes**), each of which is incapable by itself of giving rise to a new organism. The gametes are of two kinds, usually distinguishable by their behaviour even if indistinguishable in appearance. When two gametes of opposite kind meet and fuse together a **zygote** results. This is a unicellular, sexually-produced spore, the result of the fusion of two gametes. The zygote is capable of developing into a new plant under suitable conditions, sometimes immediately but more usually after a period of rest. In the latter case it is protected by a resistant cell-wall.

The *asexual* method of reproduction may also be by means of spores, but these are produced directly by the parent organism without the intervention of sexual fusion, and are capable, by themselves, of giving rise to a new organism. Different kinds of asexually-produced spores are distinguished according to the manner of their production, and their behaviour when set free from the parent. Thus spores which are motile in water are called zoospores; conidia are produced externally and exposed to air-currents, by which they are borne; other spores are encased within sporangia, which dehisce and so liberate the spores. Within the Fungi certain so-called asexual spores are produced, which undoubtedly involve a previous fusion of nuclei within the organ which bears them. Such spores, e.g. basidiospores and certain ascospores are probably more correctly regarded as related to modified sexual processes. For details of these and other spores reference will have to be made to the types described in a later section of this book.

Asexual reproduction may also be effected by the separation of a part of the parent organism, which is capable of growing directly into a new organism. This method is usually distinguished as **vegetative reproduction** or **propagation**, and is frequently made use of and encouraged in horticultural and agricultural practice. The part separated off may be a more or less specialised portion of the vegetative region, such as a potato tuber (stem), sweet potato tuber (root), corm (stem), bulb or bulbil (bud), etc. Budding, grafting, layering, etc., are horticultural extensions of this method of propagation made possible by human agency.

CHAPTER II

GENERAL HISTOLOGY

A. THE CELL

1. Cellular Structure of Plants

We have already explained (p. 5) that the substance of the plant-body is not homogeneous, but, in all except the simplest forms, consists of aggregations or unions of microscopic structures, called cells, each *living* cell consisting of a tiny mass of a viscid substance called protoplasm, bounded by a distinct membrane, the cell-wall. These cells can be seen readily by teasing out the substance of a very ripe, mealy apple in water, and examining it under the microscope; also in thin sections of stems, roots, and other parts of plants (see e.g. Figs. 64, 92) viewed under the microscope. The protoplasm is the essential, living substance of a cell, and the seat of vital processes. The cell-wall is formed by the activity of the protoplasm, and, according to the type of cell, is built up to perform special functions.

The cell-walls, therefore, are to be regarded as constituting a skeleton or framework, enclosing the living substance, and giving firmness and elasticity to the whole organism. They do not necessarily prevent communication between the living substance of the various cells, for the protoplasm of one cell may be connected with that of others by means of extremely delicate threads passing through the cell-wall. Thus the living cells of a plant are bound together in organic union, and carry on in harmony the processes necessary for the life of the plant.

In the simplest forms of multicellular plants, the organism consists of an aggregation of similar cells, all carrying on very much the same functions; but in higher forms, correlated with the physiological differentiation which has taken place, there is what is called **Histological Differentiation.** In other words, many different kinds of cells, more or less definitely arranged in groups, or tissues, can be recognised, the form and structure of the cells in each tissue being related to the functions which they perform. This differentiation becomes more and more marked as we pass from lower to higher types. In the Thallophyta and Bryophyta, all parts of the organism consist of *living* cells, although these cells may present many different forms. For this reason these two divisions are distinguished as "cellular plants."

A considerably higher degree of differentiation is exhibited by the Pteridophyta and Spermatophyta. These plants are rooted in the ground with their shoots exposed to the air, and possess elaborate arrangements for the conduction and distribution of nutritive substances. In addition to typical living cells of varied form, other cells are modified and allow the rapid transmission of fluids from the roots to the leaves or vice versa. Such specialised cells are usually associated in groups forming strands or bundles which supply the whole plant body, and are generally arranged in a definite pattern, according to the plant organ in which they are situated. These strands, concerned with conduction of fluids, are called vascular bundles, and together they form the vascular system of the plant. The Pteridophyta and Spermatophyta are referred to as "vascular plants" because they possess these vascular tissues.

Other cells may be modified in such a way that they give added strength to those organs which require it. Individual cells, or groups of cells forming a tissue, may be wholly given up to this function. Their cell-walls are strengthened, their form altered during development, and they may lose their living protoplasm, in which case they are dead. They are advantageously placed so as, for example, to give support to a stem which not only has to stand erect and bear the weight of its leaves and branches, but has to withstand strains brought to bear on it by external influences such as wind. Such tissues are referred to as mechanical tissues.

As we proceed we shall see that certain tissues may perform more than one function. Thus a tissue may be vascular and also mechanical.

The cellular structure of plants was first recognised by Robert Hooke and recorded in his *Micrographia*, published in 1667. He observed a resemblance between the microscopic structure of ordinary bottle-cork and the cells of honeycomb, and introduced the term "cell" in this sense. In further microscopic study attention became focused on the cell-wall and different types of cell were distinguished by differences in cell-wall structure. Later investigators have shown that the living contents of the cell, the protoplast, are of fundamental importance, and that the cell-wall is a product of the vital activity of the protoplast. Some protoplasts can, and, in fact, do exist without a cell-wall. With this advance in knowledge the concept of the cell changed, and the term "cell" came to be applied to the protoplast, whether "naked" or bounded by a cell-wall. As generally used, however, the term "cell" ranges between these two extremes; that is, it applies to a naked protoplast, to a protoplast and its cell-wall, and to a cell-wall which is the product of a protoplast, but within which the latter has died.

2. The Young Cell

Cells arise from pre-existing cells by a process of cell-division. All plants begin life as a single cell. They may remain unicellular, or become multicellular as the result of repeated cell-division. As we pass from the lower to the higher plants, along with the increasing size and complexity of the plant-body, we find that cell-division becomes localised. All living cells are potential dividing cells, but cells which have become specialised for various functions do not usually divide further unless stimulated to do so, as by wounding. In the higher plants dividing-cells are found, particularly at the tips of roots and stems, which are consequently termed the growing points. In members of the Bryophyta and Pteridophyta a single apical cell of definite form may repeatedly divide. In the Spermatophyta two or more layers of cells may be concerned. Such cells are said to be meristematic, and the growing points primary meristems. Secondary meristems may arise later in living cells which have originated from the primary meristems.

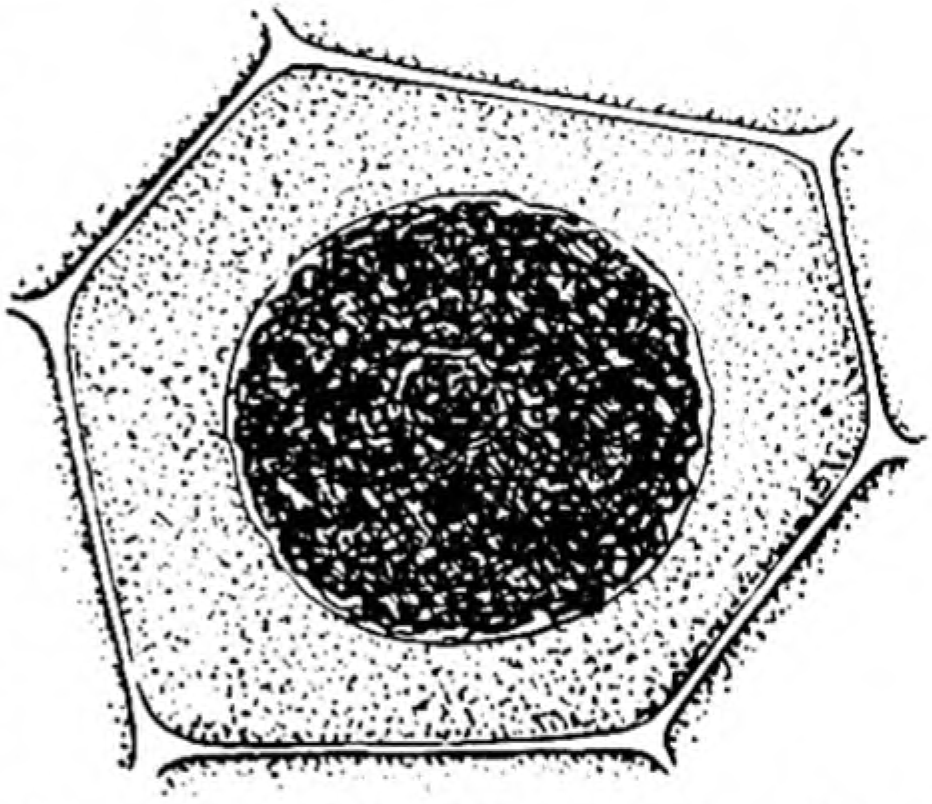


Fig. 4. Meristematic Cell, Resting Condition.

The growth of the multicellular plant-body depends, in the first place, on cell-division, then on the enlargement of the cells thus produced, and their differentiation and adoption of various functions.

In order to examine the structure of a meristematic cell it is necessary to cut thin sections, e.g. of a root-tip, and examine them under the high magnification of a compound microscope. Transverse and longitudinal sections are required to give a complete picture of the individual cell. In longitudinal section it may appear more or less rectangular, and in transverse section it may be rectangular or several-sided. In the solid, therefore, it is shaped something like a prism or truncated pyramid with four or more sides, the short axis parallel to the axis of the root.

The meristematic cell is bounded by a thin cell-wall and contains the protoplast. The latter consists of a relatively large central nucleus and the surrounding cytoplasm. Within the cytoplasm are suspended specialised protoplasmic bodies called plastids or chromatophores, and non-living inclusions in the form of minute granules and droplets.

3. The Protoplasmic Substance

Observation of the living cell indicates clearly that the *protoplasm* is not homogeneous, but its physical nature is still rather a matter for conjecture. There is little doubt, however, that it is a colloidal system, usually with many of the properties of a liquid, being in fact a liquid (sol) in which are dispersed either liquid or solid particles which are either aggregates of small molecules, or are very large molecules. The particles dispersed in the continuous liquid phase of the protoplasm are extremely minute, and often only just visible with the most powerful microscope. Many of the properties of the protoplasm are the outcome of its colloidal nature.

Chemically, the dry substance of the protoplasm appears to consist mainly of proteins with appreciable amounts of fats and fatty substances and of carbohydrates, and smaller amounts of other organic compounds and of mineral matter. Analysis of the protoplasm always, of course, includes any substances present in it at the time, that is, both living and non-living protoplasmic inclusions. But it must be remembered that methods of chemical analysis bring about the death of the protoplasm, and so the analysis is really of *dead*, and not living protoplasm.

The analyses do, however, show the presence of substances (fat-like compounds and proteins) which it is known are capable of forming the disperse phase in a colloidal system. The evidence of chemical analysis and of observation on the physical properties of the protoplasm suggest that in the protoplasm we have a continuous phase of water containing proteins and fatty substances, and dispersed in this are granules (solid or liquid) of protein, either alone or united with other substances, the whole being of the consistency of a slightly viscous liquid.

We pointed out in Chapter I that the surface layer of the protoplasm differs from the inner part, and in a system such as that outlined above we might expect to find in the outermost layers a concentration of fatty substances. Any such surface layer is certainly of a complex nature and of vital importance, as its properties will govern the entry of substances into, and their exit, from the protoplasm.

4. The Nucleus

The *nucleus* of the meristematic cell may be observed in the resting condition or in any of the various stages of nuclear division. Recent work on nuclear structure appears to show that two types of resting nucleus occur in different plants. One type is known as the "solid" nucleus, the other as the "pro-chromosomal" or vesicular type. It must be borne in mind, however, that detailed study of nuclear structure is only possible, so far, as the result of first "fixing," then sectioning the meristematic tissue. The sections have to be "stained" with certain dyes. Technique, as well as treatment, plays an important role in this process: choice of fixative and of stain, amount of staining and, above all, resolving power of the microscope at high magnifications are all fundamental to successful interpretation of what is observed. Moreover, certain observed phenomena may be the result of treatment, and recorded observations must make all due allowance for these.

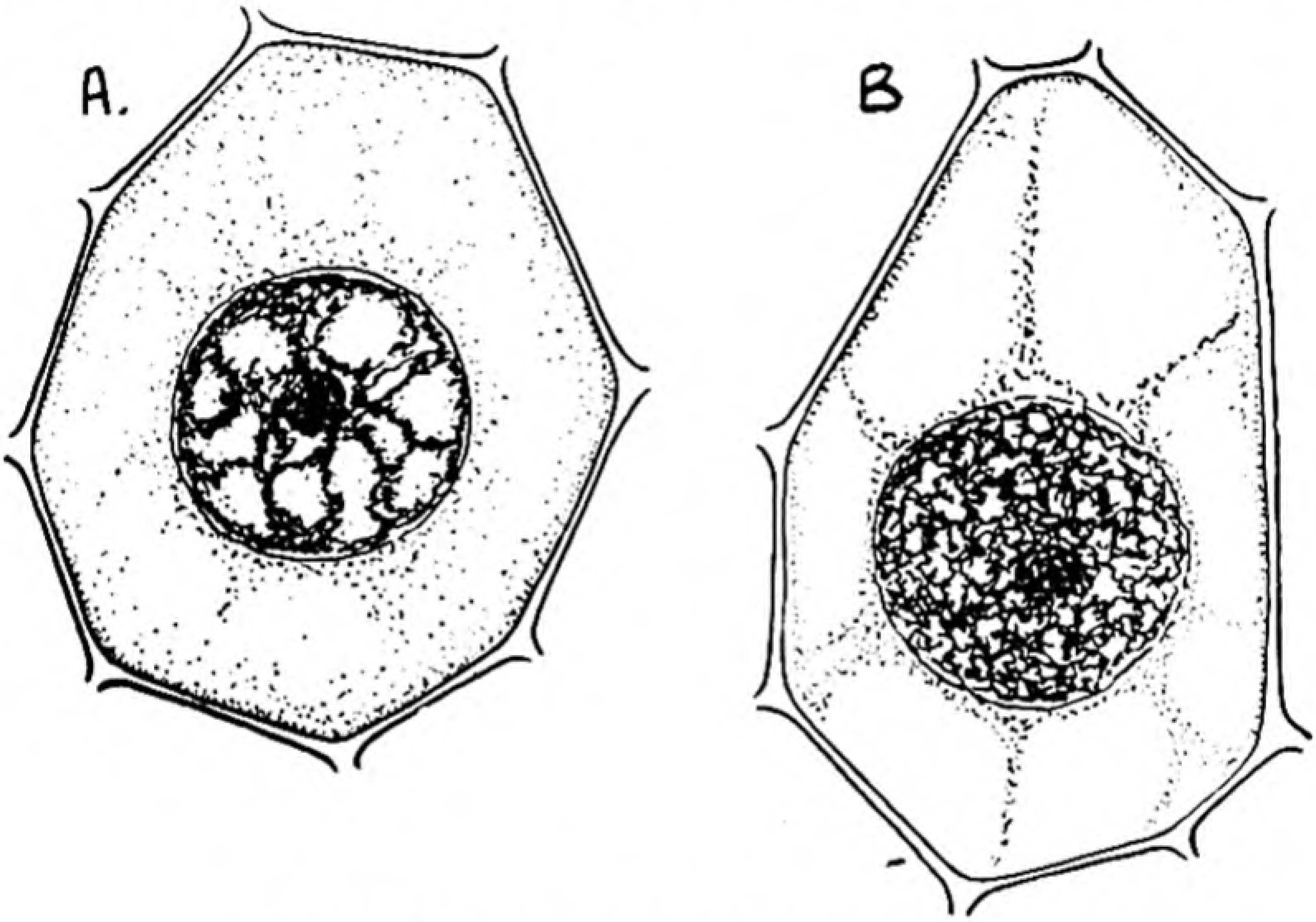


Fig. 5. Two Types of Resting Nucleus.
A, Prochromosomal. B, Solid.

The prochromosomal type of nucleus (Fig. 5, A) consists of a vesicle of sap around the periphery of which is the whole of the stainable material of the nucleus, the chromatin, included in relatively small bodies called prochromosomes. One or more nucleoli are also present.

The " solid " type of resting nucleus (Fig. 5, B) is devoid of free sap and, after fixation, has the appearance of a uniform meshwork of chromatin filling the whole nucleus except for the space occupied by one or more nucleoli. The latter, at least in the early stages, are fluid. This type of nucleus is found in members of the Liliaceae, in *Vicia* and *Osmunda* (the royal-fern). The chromatin meshwork is frequently referred to as a " reticulum," composed of " karyotin."

The nucleus plays an important part in governing the metabolic processes which go on within the cell, resulting in cell-division, growth and differentiation. The nucleus also contains the hereditary characters which are passed from parent to offspring.

5. The Cytoplasm

In mature living cells the *cytoplasm* (that part of the protoplasm distinct from the nucleus) forms a lining to the cell-wall. Internally the cytoplasm is in contact with the contents of the vacuole, and externally with the cell-wall and the liquid with which it is saturated. The cytoplasm is not homogeneous. On physical grounds we should expect the surface layers of the cytoplasm to differ in composition and structure from the innermost parts, a knowledge of the laws of surface tension leading us to expect an accumulation of the fat-like components of the cytoplasm at the surface. The differentiated limiting layers frequently visible in animal cells and called the ectoplasm, but rarely observed in plant cells, form the plasma membranes. Although the specially differentiated plasma membranes are but rarely visible in plant cells, there is experimental evidence of their widespread existence. The innermost part of the cytoplasm (endoplasm) contains specialised protoplasmic bodies and non-living inclusions.

The most conspicuous protoplasmic bodies are the plastids. In young meristematic cells they are minute, and have been called proplastids. They multiply by direct division, either at this stage or at cell maturity. When a cell divides, proplastids are present in the cytoplasm of each daughter cell, and as the daughter cell grows the proplastids mature. Mature plastids are classified somewhat arbitrarily according to their colour into two chief types; chromoplasts, which are coloured, and leucoplasts which are colourless.

6. Chromoplasts

It is advisable to apply this term to all plastids containing one or more pigments, although the term is in general use as applying to all plastids whose pigments are other than green. Green chromoplasts are called *chloroplasts*. Specialised chloroplasts such as occur in some Algae (e.g. *Spirogyra*) are sometimes called *chromatophores*.

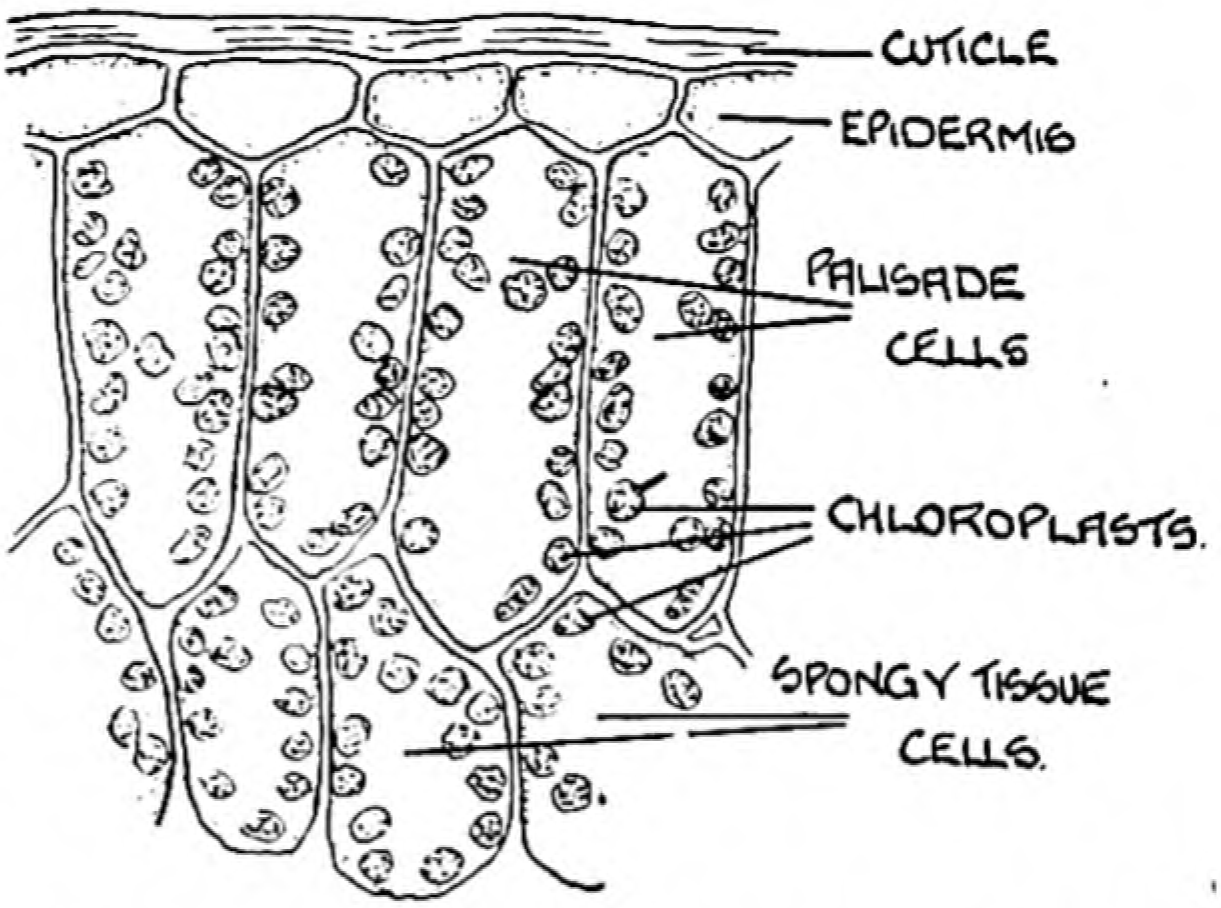


Fig. 6. CHLOROPLASTS IN PALISADE CELLS OF LEAF OF *Andromeda*.

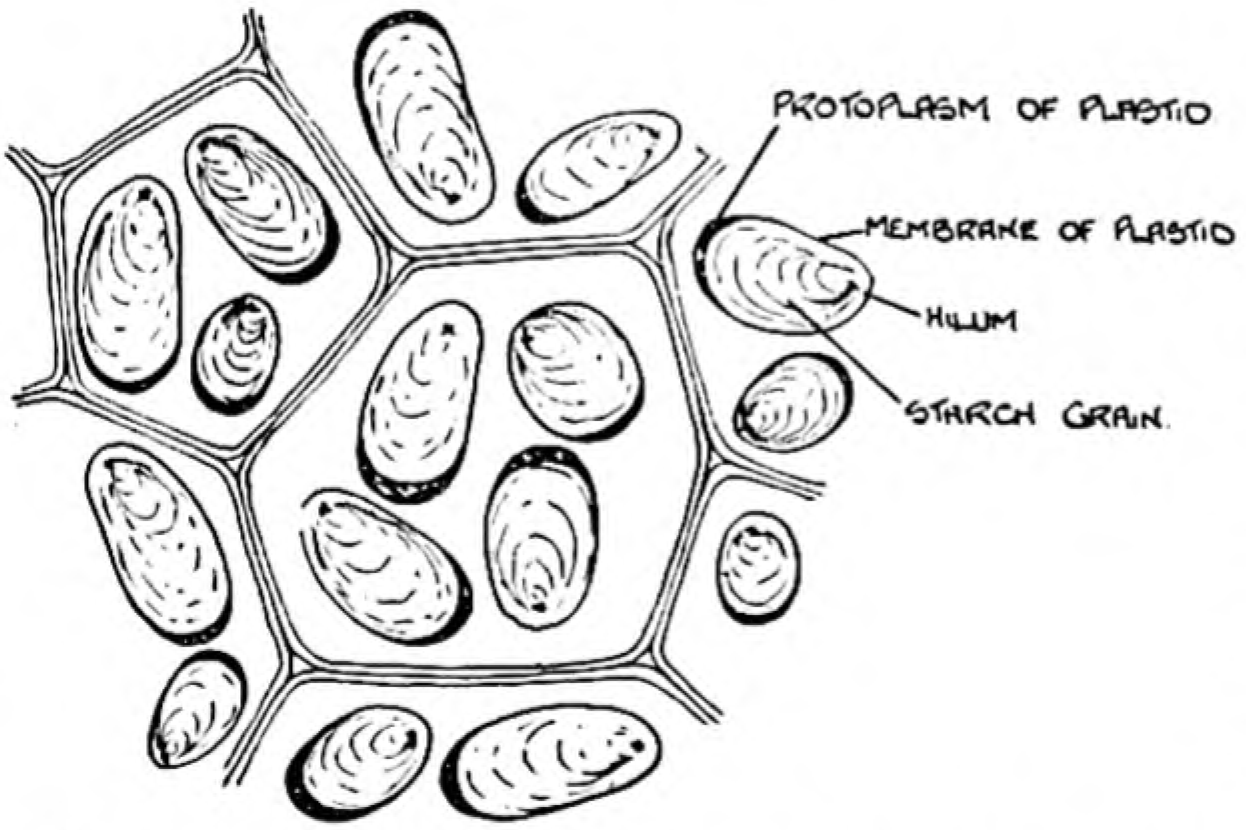


Fig. 7. STARCH GRAINS INSIDE THE PLASTIDS OF *Pellionia*.

CHLOROPLASTS.—These plastids contain the green pigment chlorophyll. They are usually rounded, discoid or more or less spherical bodies, but in the Algae have characteristic shapes. Green plants owe their colour to the numerous chloroplasts which are found in the cells of the leaves and young stems (Fig. 6). They appear uniformly green to the naked eye, but under the microscope the chlorophyll is seen to be restricted to the chloroplasts, and not diffused throughout the cell. Chlorophyll rarely develops within the plastid in the absence of light, but in the presence of light the chloroplast appears to be the seat of carbohydrate synthesis. The end product of this photosynthesis is generally starch, which takes shape as a starch grain within the body of the chloroplast (Fig. 7). Starch is the first visible product of photosynthesis, and can be detected by its reaction with solution of iodine in potassium iodide. After a few hours' exposure to light the chloroplasts of a leaf usually contain starch. If the leaf is detached from the plant, killed by immersion in boiling water, the chlorophyll extracted by dissolving it out with alcohol, and the leaf then soaked in a solution of iodine, it becomes an almost black colour, due to the "assimilation" or "temporary" starch still in the chloroplasts. During the hours of darkness this starch is transformed into soluble sugars by enzyme action, and is transported, or translocated, to regions where growth is taking place, where it is utilised by the protoplasm for building up new plant substance; or it may go to storage organs and be reconverted into "storage" or "reserve" starch; this conversion being accomplished by the activity of the *leucoplasts*.

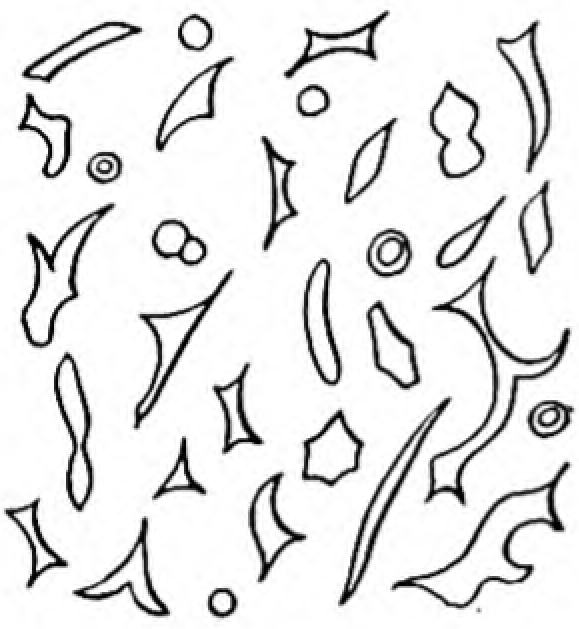


Fig. 8. CHROMOPLASTS FROM *Capsicum* FRUIT.

Other chromoplasts have colours ranging from red to yellow and vary in shape, sometimes being sharply angular, due to crystallisation of the pigment within the plastid. Such plastids give the characteristic colour to many petals, and fruits, but they also occur in some underground organs such as carrots, and their function is not altogether clear. Not all colour in plant organs is due to chromoplasts; it is frequently due to coloured cell-sap, as we shall see.

LEUCOPLASTS.—The proplastids of meristematic cells may develop into colourless *leucoplasts*, especially in underground organs and the deeper-seated tissues of multicellular plants. When mature they may be rounded or spherical like the chloroplasts, or elongated or rod-like. Leucoplasts may develop chlorophyll and function as chloroplasts, as, for example, when potato tubers are lifted and exposed to light. Leucoplasts that are concerned with the storage of reserve starch are called *amyloplasts*. These amyloplasts are supplied with sugars

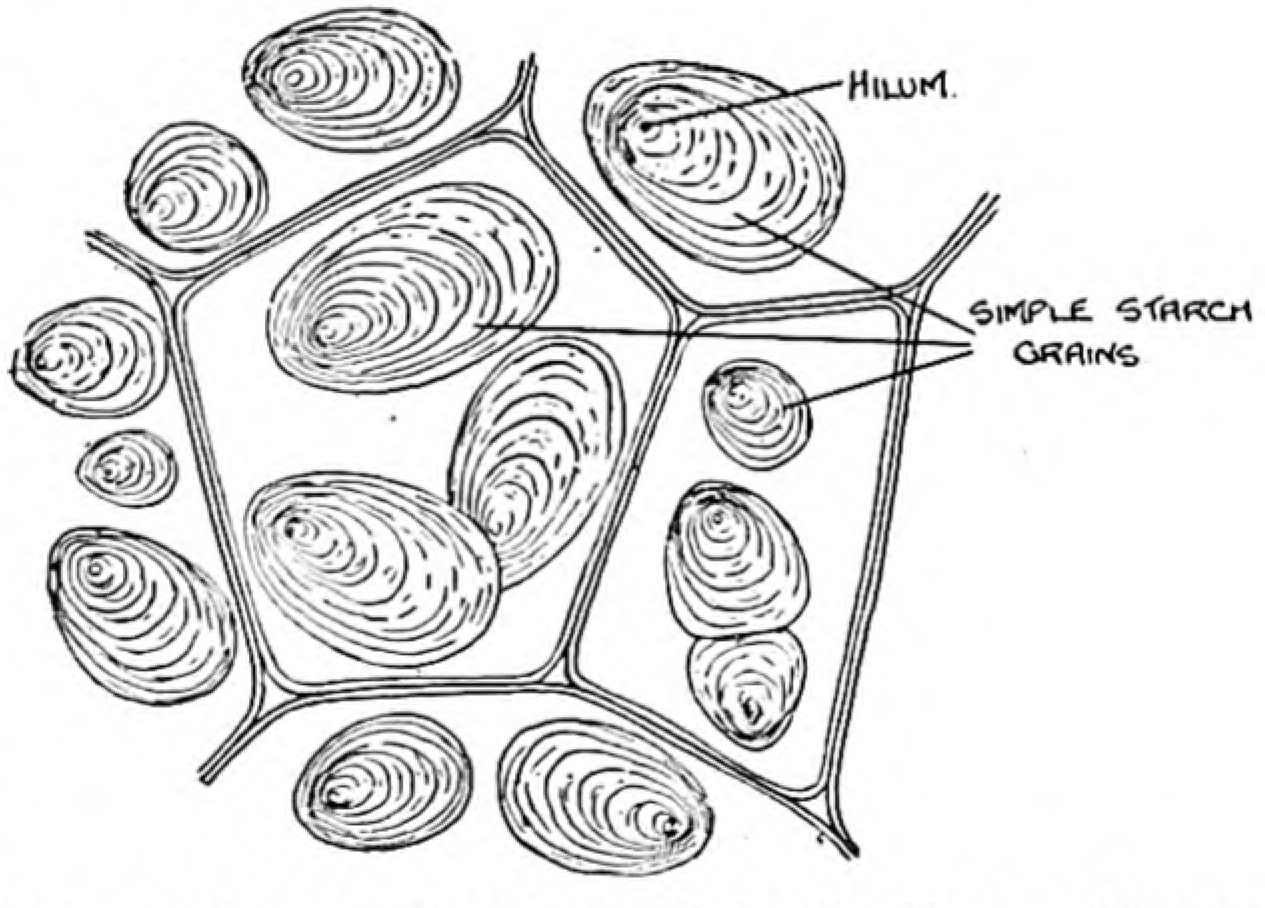


Fig. 9. STARCH GRAINS IN CELLS OF POTATO TUBER.

from the green parts of the plant and utilise them for the building up of starch grains inside the amyloplast (Fig. 9).

The starch grains may be simple or compound. Simple starch grains vary in form, size and markings. In some a point, or a radiate cleft, marks the hilum, which may be central or eccentric or even at one end. Arranged round this, striations of varying density may be seen, but quite frequently they are not visible. Compound starch grains may have few to many components, which, when separated, may each have a hilum and be somewhat angular in shape, due to mutual pressure during development within the membrane of the amyloplast. Starch grains are sufficiently characteristic to make it possible for the expert to determine their botanical source. On this account they afford a useful criterion when flours, powdered drugs, etc., are examined microscopically in order to detect adulteration. Recent research indicates that the starch molecule consists of about 25 glucose molecules linked together (with elimination of water), and the differences in starches from various plants are probably due to differences in the arrangement of the starch molecules in the starch grain.

Viewed under polarised light with crossed Nicols the starch grain shows a dark Maltese cross whose centre is at the hilum, against a light background. The grain is crystalline, and minute grains can be picked out quite readily, using a polarising microscope. By this means the beginnings of starch formation inside chloroplasts can be detected after a few minutes' exposure to light.

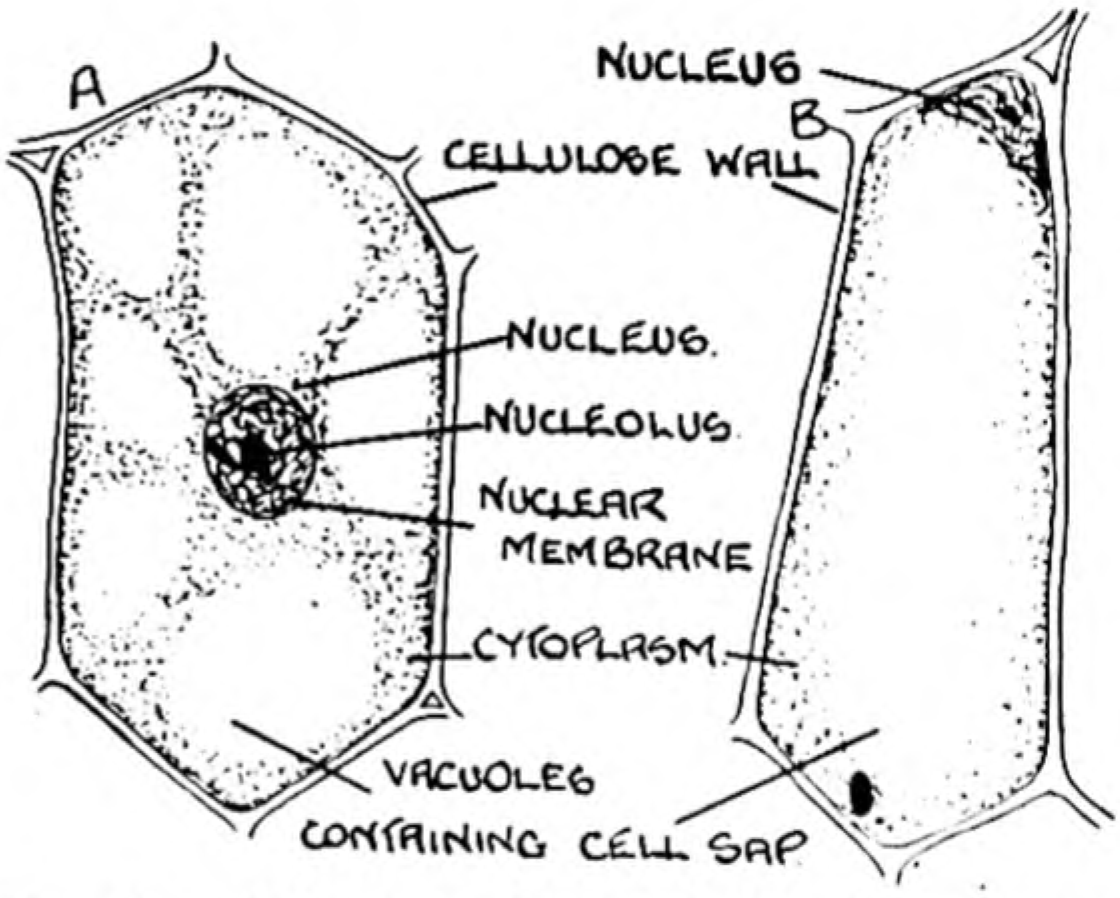


Fig. 10. TYPES OF VACUOLATED CELL FROM FERN RHIZOME.

A, "Suspended" nucleus. B, Peripheral nucleus.

Starch grains are insoluble in cold water. Treated with solution of iodine in potassium iodide they stain a dark blue or violet colour.

7. Vacuoles

We have noticed already that the cytoplasm of meristematic cells contains non-living inclusions. Some of these are in the form of minute droplets. Each droplet is a small vacuole filled with cell-sap. These small vacuoles enlarge and finally coalesce, so that ultimately one large vacuole is formed. The enlargement of the vacuoles is accompanied by the entry of water into the cell. Therefore it will be evident that with the entry of water into the cell, the size of the cell will increase, and, in fact, the cell attains a volume many times greater than the volume of the original meristematic cell. During this process of cell enlargement by vacuolation the nucleus and cytoplasm do not greatly increase in size, and in the fully vacuolated cell the cytoplasm forms a parietal layer which lines the cell-wall internally, and a number of strands which extend from this parietal layer across the central vacuole. The nucleus may be suspended in the centre of the vacuole by these cytoplasmic strands, or it may be embedded in the parietal layer of cytoplasm. This layer of cytoplasm is sometimes referred to as the primordial utricle, and besides the nucleus it contains plastids, and often various non-living inclusions as well. When cell enlargement is proceeding, the cell-wall is tightly stretched and becomes increased in area, whilst its thickness is maintained or even increased by the deposition of cellulose (generally), formed by the activity of the living protoplasm.

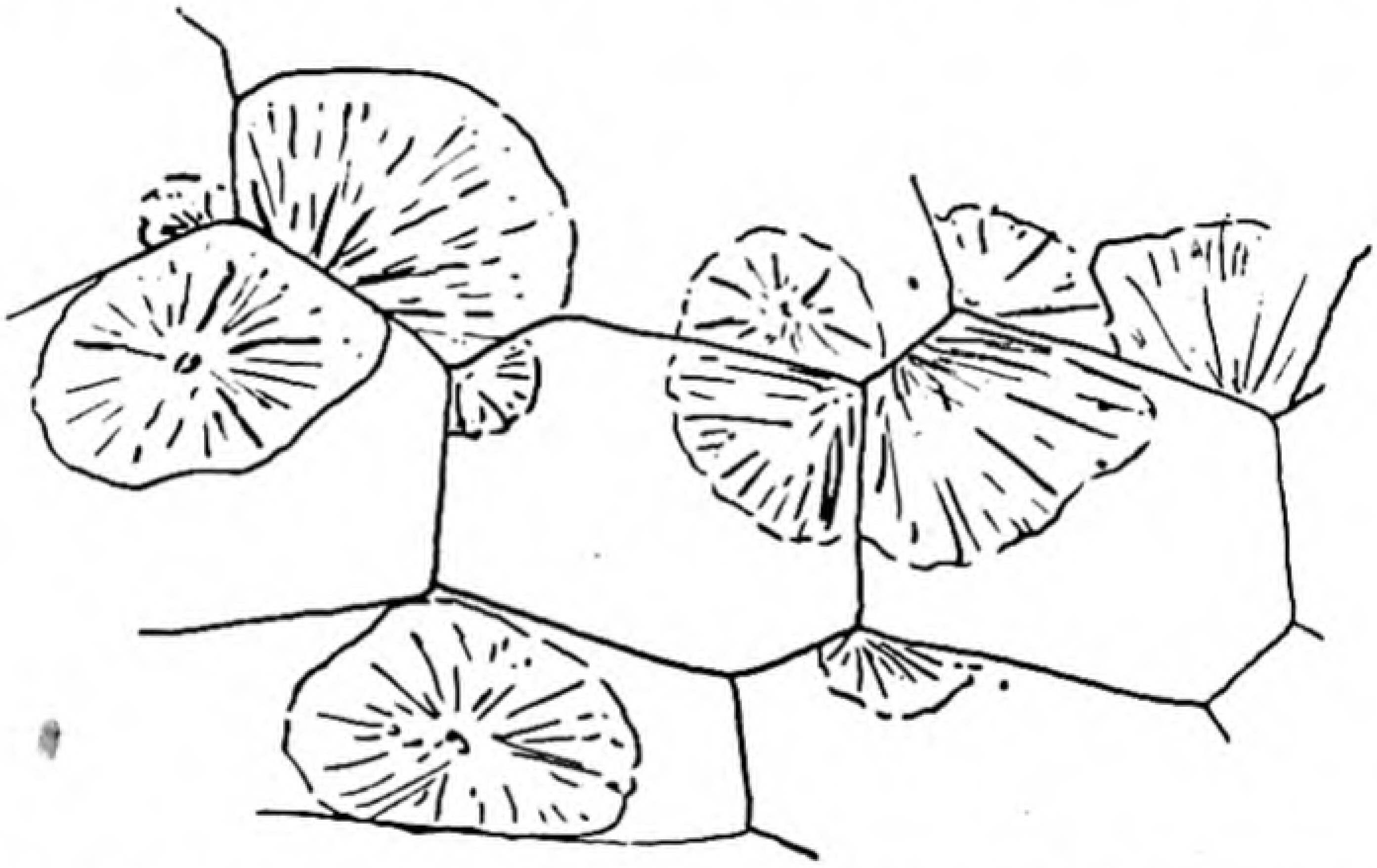


Fig. 11. SPHAERITES OF INULIN IN SECTION OF DANDELION ROOT PRESERVED IN ALCOHOL.

The cell-sap which fills the vaçuole consists of an aqueous solution of various inorganic and organic compounds. Inorganic ions are always present, especially those resulting from the dissociation of the nitrates, sulphates and phosphates of certain alkaline and alkaline-earth metals, and carbon dioxide in solution is also present.

A number of sugars have been isolated from the cell-sap of various plants. Glucose (dextrose) and fructose (laevulose), monosaccharides with the empirical formula $C_6H_{12}O_6$, are especially common, small amounts of glucose being found in most leaves which are exposed to light, and larger amounts in many fruits. These sugars readily reduce Fehling's solution and ammoniacal silver nitrate, and they share this reducing property with a disaccharide, maltose ($C_{12}H_{22}O_{11}$), which is sometimes present in the sap of leaf cells. Sucrose, or cane sugar ($C_{12}H_{22}O_{11}$), is a non-reducing disaccharide widely distributed in plants, being abundant notably in the root of the sugar-beet and the stem of the sugar-cane. These form the commercial sources of " cane sugar."

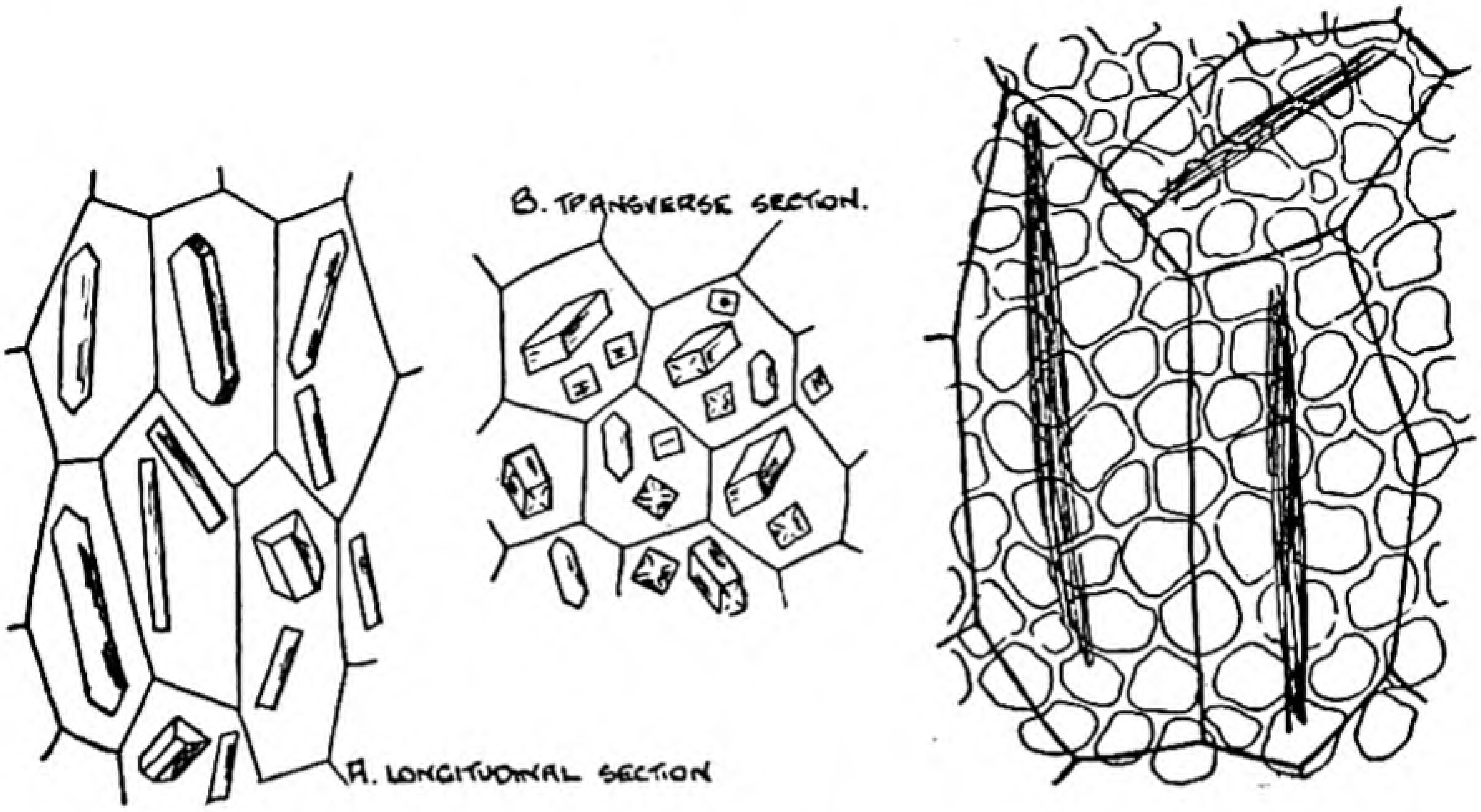
A complex, soluble polysaccharide, inulin, occurs in the cell-sap of the tubers of dahlia and Jerusalem artichoke and in the root of the dandelion. Although soluble in water inulin is insoluble in alcohol, and hence when inulin-containing tissues are preserved in alcohol, the inulin is precipitated in the cells in the form of sphaerites (sphere crystals).

Other carbohydrates of less common occurrence in the cell-sap include dextrin, mannitol and various pentosans, whilst soluble pectin, which is believed to be a compound of certain sugars with other substances, sometimes occurs in appreciable amount.

Glycosides are also of common occurrence in the cell-sap. These may be regarded as compounds of glucose, generally with aromatic substances, so that when the glycoside is decomposed, and the aromatic substance set free, an aromatic smell is discernible. An example is amygdalin in the bitter almond. This, when decomposed, gives rise to glucose, benzaldehyde, and hydrocyanic acid, and it is to the benzaldehyde particularly that the characteristic odour and taste of bitter almonds is due. Indeed, artificial almond essence consists mainly or wholly of synthetic benzaldehyde. These glycosides are decomposed by enzymes, and generally the appropriate decomposing enzyme is present in the same tissue, but not necessarily in the same cell, as the glycoside. Thus, in bitter almonds the enzyme emulsin splits up the amygdalin. The glucose set free by the decomposition of the glycoside can, in all probability, be utilised by the plant in its metabolism.

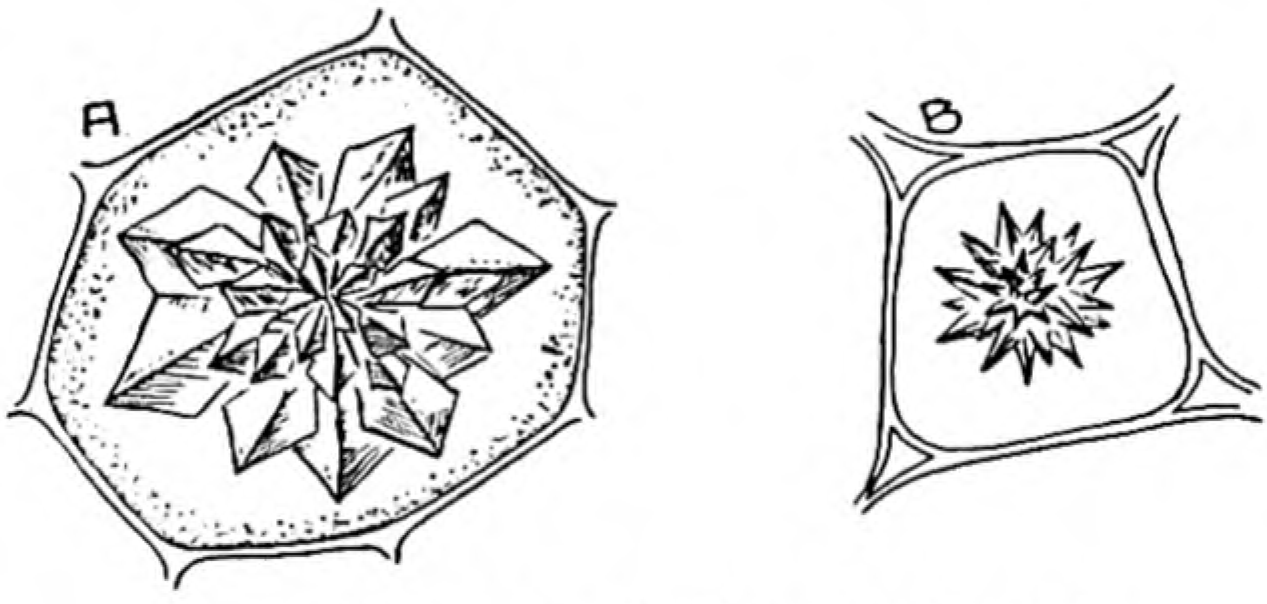
Mucilaginous compounds occur in cell-sap, too, and it is to these compounds that the slimy character of many cell-saps is due. Mucilages are found abundantly in the cell-sap of many bulbs, e.g. onion, bluebell, and in the leaves of many succulent plants, and, as we shall see later, are also formed from cell-walls. Mucilages swell or dissolve in water, but are insoluble in alcohol. They are polysaccharide in nature and, when hydrolysed, may yield sugars which reduce Fehling's solution. Reagents in common use for testing for mucilages are solution of ruthenium red, alkaline solution of corallin, dilute solution of methylene blue and chlor-zinc iodide.

Tannins may be present in cell-sap. Treated with ferric salts they give either a blue-black or green colour. They are complex substances, and are classified according to their behaviour when treated with boiling dilute sulphuric acid. They are soluble in water and alcohol and are best examined after extracting, but if it is desired to examine them *in situ*, the plant tissue containing them

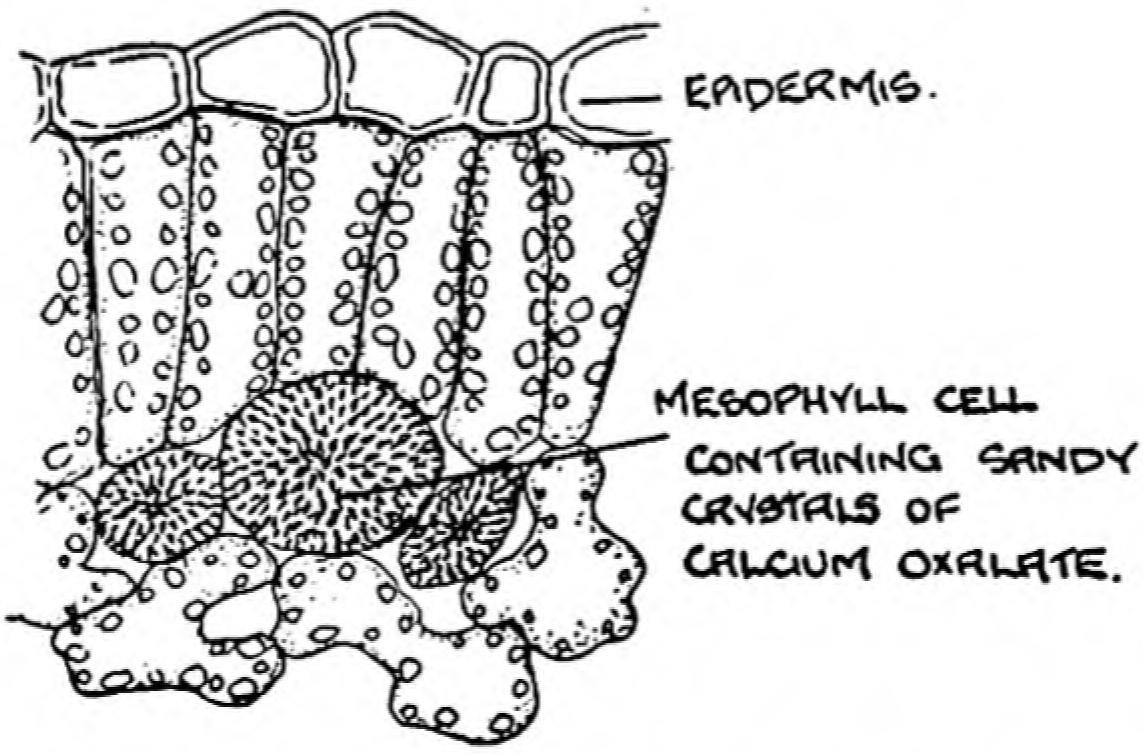

B. TRANSVERSE SECTION.
A. LONGITUDINAL SECTION

(*a*) Prismatic Crystals in the phloem of *Quillaja Saponaria.*

(*b*) Raphides in leaf-cells of *Circaea Lutetiana.*



(*c*) A and B, Druses in *Rheum* and *Begonia.*


EPIDERMIS.
MESOPHYLL CELL CONTAINING SANDY CRYSTALS OF CALCIUM OXALATE.

(*d*) Sandy Crystals in leaf of *Atropa Belladonna.*

Fig. 12. TYPES OF CALCIUM OXALATE CRYSTALS.

should be sectioned dry and mounted direct in the reagent, e.g. dilute solution of ferric chloride.

Anthocyanin pigments are frequently present in cell-sap. These pigments as a rule give blue or red (or intermediate) colours to the cell-sap, and are the cause of many floral colorations; whilst a similar type of compound is responsible for the red coloration of the root of the garden beet.

The cell-sap is often acid in reaction, either because of the presence of free organic acids, or their acid salts. Malic, citric and tartaric acids are all of common occurrence, and the acidity of many fruits is due to the presence of these acids in the cell-sap. Oxalic acid, too, is of general occurrence, but it is usually present, not as the free acid, but in the form of its insoluble calcium salt, and as such is usually regarded as a waste product of cell metabolism, and of no further use to the plant, whereas the other organic acids mentioned may be used in respiration or in other ways.

Calcium oxalate occurs in a crystalline form, and the crystals may be of various types, the commonest belonging to the monosymmetric (monoclinic) system. These crystals are widely distributed in plant tissues in the form of:—

(1) Single crystals, e.g. square prisms, double pyramids, rhombohedra, etc. Sometimes these are so large as to fill the cell, distorting the cell-wall to their shape. The cells containing these crystals may be scattered throughout a tissue, as in Quillaia bark or Quassia wood, or they may be arranged as a crystal sheath around bundles of sclerenchymatous fibres as in Cascara bark and Liquorice root, or vascular bundles as in Senna leaf. Included under single crystals are needle-shaped (acicular) ones named raphides, usually associated together in bundles in enlarged parenchymatous cells containing mucilage. Such bundles of raphides are particularly met with in Monocotyledons.

(2) Druses, cluster- or rosette-crystals, which are spheroidal groups of tetragonal crystals, frequently built up around an organic core. Large druses are present in *Rheum*, and minute ones, associated with aleurone grains, in the endosperm cells of fruits of Umbelliferae.

(3) Crystal-sand, masses of micro-sphenoidal crystals packed into a cell. Examples are seen in leaves and roots of *Atropa Belladonna*.

Crystals of calcium oxalate dissolve in any of the mineral acids without effervescence; they are insoluble in dilute acetic acid, even on warming. Dilute hydrochloric and acetic acids are therefore employed in microchemical tests for calcium oxalate. By this means it is distinguished from calcium carbonate, which dissolves in dilute acetic acid.

Calcium carbonate occurs only infrequently in plants; it is best known in those curious structures called cystoliths, which consist of a peg-like ingrowth of the cell-wall into the cavity of epidermal cells of *Ficus* leaf. In and around this protrusion calcium carbonate is deposited. Cystoliths are found mainly in the members of the families Moraceae and Acanthaceae, and may be stalked or sessile.

Soluble nitrogenous compounds may be present in the cell-sap. We have mentioned already that inorganic nitrates may occur. Ammonium compounds may be present too, and also relatively simple organic compounds of the nature of amino acids and amides, and some of these may represent steps in protein synthesis.

Besides the proteins which form a part of the living protoplasm, nonliving proteins may occur either dissolved in the cell-sap or in the form of crystal-like bodies, crystalloids. In many seeds, especially those containing oil, the vacuoles contain large amounts of dissolved proteins, and as the seed dries out and ripens these proteins may be transformed into *aleurone grains*. Each grain has a membrane, and this encloses a mass of protein in which bodies are embedded. One of these, the larger, is the crystalloid, which consists of protein. The other globoid bodies, which are smaller than the crystalloid, consist of protein combined with phosphates. Treatment with solvents resolves the aleurone grain into its components. Cold water dissolves away the ground matter of the grain, leaving the crystalloid and globoids inside the membrane. Dilute caustic potash slowly dissolves the membrane and the crystalloid, leaving the globoids unaffected.

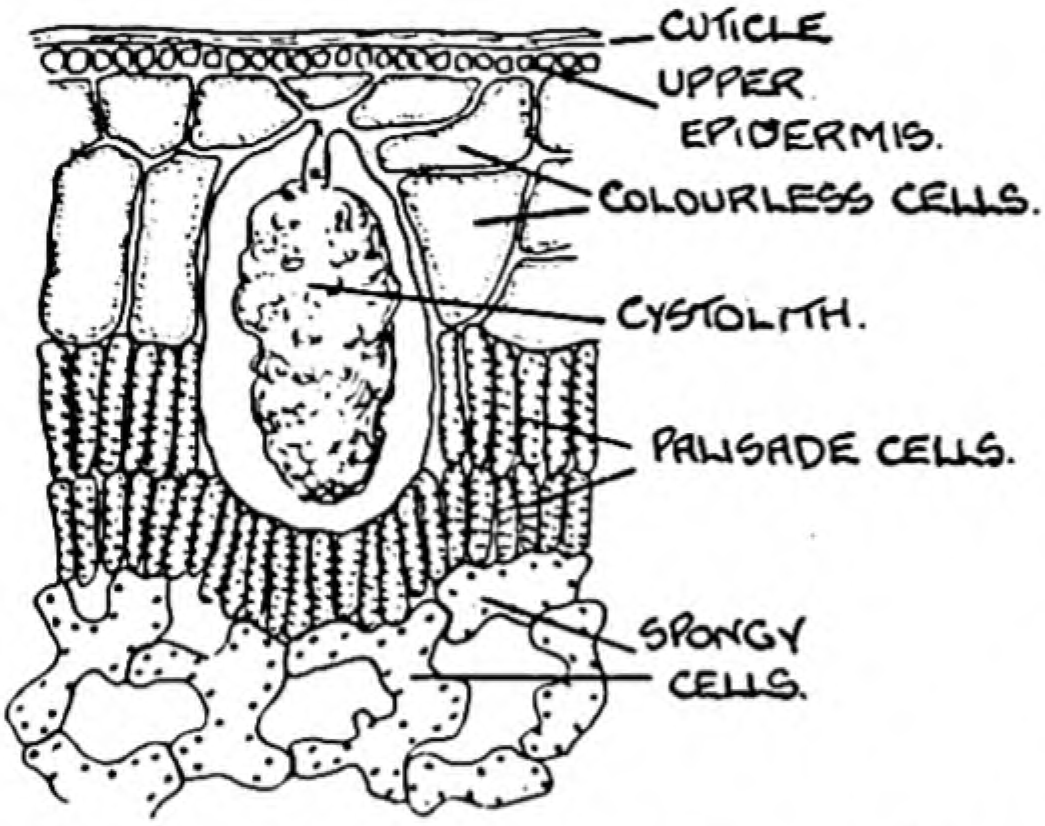


Fig. 13. Cystolith in Leaf of *Ficus*.

Fats and *oils* are frequently present in plant cells, especially in certain seeds. They occur as droplets or globules, and may be present either in the cell-sap or protoplasm, or both. Fats and oils are compounds of glycerol and various fatty acids, mainly oleic, palmitic and stearic acids, and they often form an important kind of food reserve. Similar chemically, fats and oils differ only in their consistency, fats being solid at ordinary temperatures, and oils liquid. Fats and oils found in plants are generally liquid, but there are a few exceptions. Cocoa butter, from cocoa "bean," and the fat from the seeds of the nutmeg both have high melting points and are solid at normal temperatures, but in the plant they are probably present, not as solid fat particles, but in the form of an emulsion. Microscopically, fat globules may be distinguished by their reactions with certain stains. They stain red with tincture of alkanna, Soudan III, and Scharlach R.

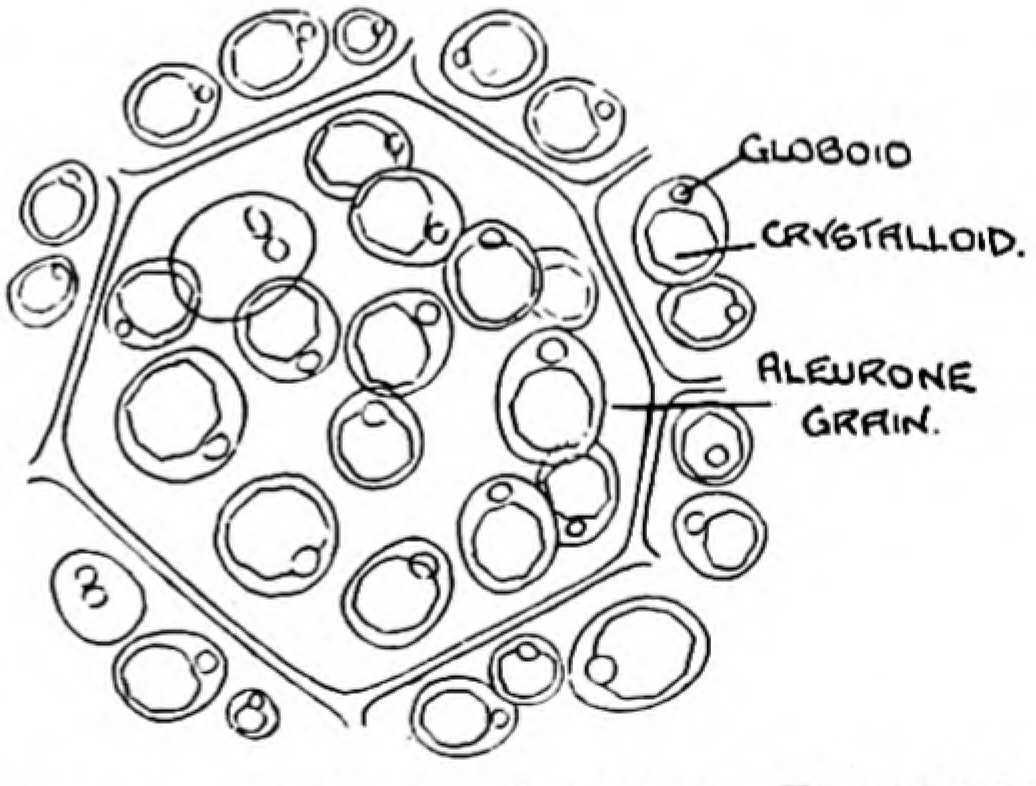


Fig. 14. Aleurone Grains in Endosperm Cells of Castor-oil Seed.

D/Prakash

We have by no means exhausted the possible constituents of the cell-sap, but have dealt briefly with the most important ones. Other substances sometimes present include various organic basic substances such as the purine bases and the alkaloids. The functions of these in the plant are not clear, but the alkaloids at least are of considerable therapeutic value.

Resins are found also, but are of limited distribution, being confined to special cells or ducts in certain plants, and odorous ethereal or essential oils are produced by some plants. These essential oils are usually mixtures of complex organic compounds such as alcohols, esters, ketones, aldehydes and hydrocarbons, not all of which are sweet smelling. Essential oil of lemon, for instance, consists mainly of inert hydrocarbons, whilst the smell and taste are due chiefly to a small amount (about 5%) of the aldehyde citral which it contains.

Resin also is not itself a simple chemical substance, but a mixture of substances insoluble in water and containing resin acids, resin esters and resenes, all of which are complex substances of high molecular weight. The relative proportions of these compounds vary in different resins. Colophony contains a high proportion of resin acid (abietic acid). Myrrh also is rich in resin acids. Benzoin, Storax, Balsams of Peru and Tolu, and Asafœtida consist mainly of resin esters and free aromatic acids. Sandarac and Mastic contain a considerable proportion of resenes.

8. Mitosis

So far we have considered the protoplast and its possible inclusions, and the vacuole. Before passing to the cell-wall it will be convenient at this stage to trace in detail the changes which take place in the protoplast of a meristematic cell in the process of division in order that we may follow the development of the cell-wall from its inception.

The first changes appear in the nucleus, and nuclear division (*mitosis*) precedes cell division. For convenience in description the stages in nuclear division have been classified under four phases: prophase, metaphase, anaphase, and telophase.

The behaviour of the "solid" type of nucleus, with its "reticulum" of karyotin, and one or more nucleoli is that which is most generally described. The "reticulum" appears to break up into separate threads, called chromosomes, the number of which is normally constant in all the vegetative (somatic) cells of a given species. At this stage (*prophase*) the chromosomes show at least a double structure, as though longitudinally divided. During prophase the nucleoli disappear, and each chromosome may assume a definite and characteristic form. The nuclear membrane disappears and fine fibrils form a "*bipolar spindle*," with the chromosomes arranged in an equatorial plane (*metaphase*). At a definite point in each chromosome, the *centromere*, two spindle fibrils appear to be attached, one to each half of the split chromosome. One of these fibrils runs from the centromere to one pole of the spindle, the other fibril to the opposite pole. The two halves of each chromosome now begin to separate, at the centromere first, then gradually along their whole length, and move towards opposite poles (*anaphase*). At the poles the daughter chromosomes now form two compact groups (*telophase*) and each group assumes the "reticulate" appearance of the parent nucleus, provided with nucleoli. Each daughter nucleus is thus a replica of the parent nucleus. It may provide the basis for a new prophase, or it may pass, temporarily or permanently into a quiescent stage.

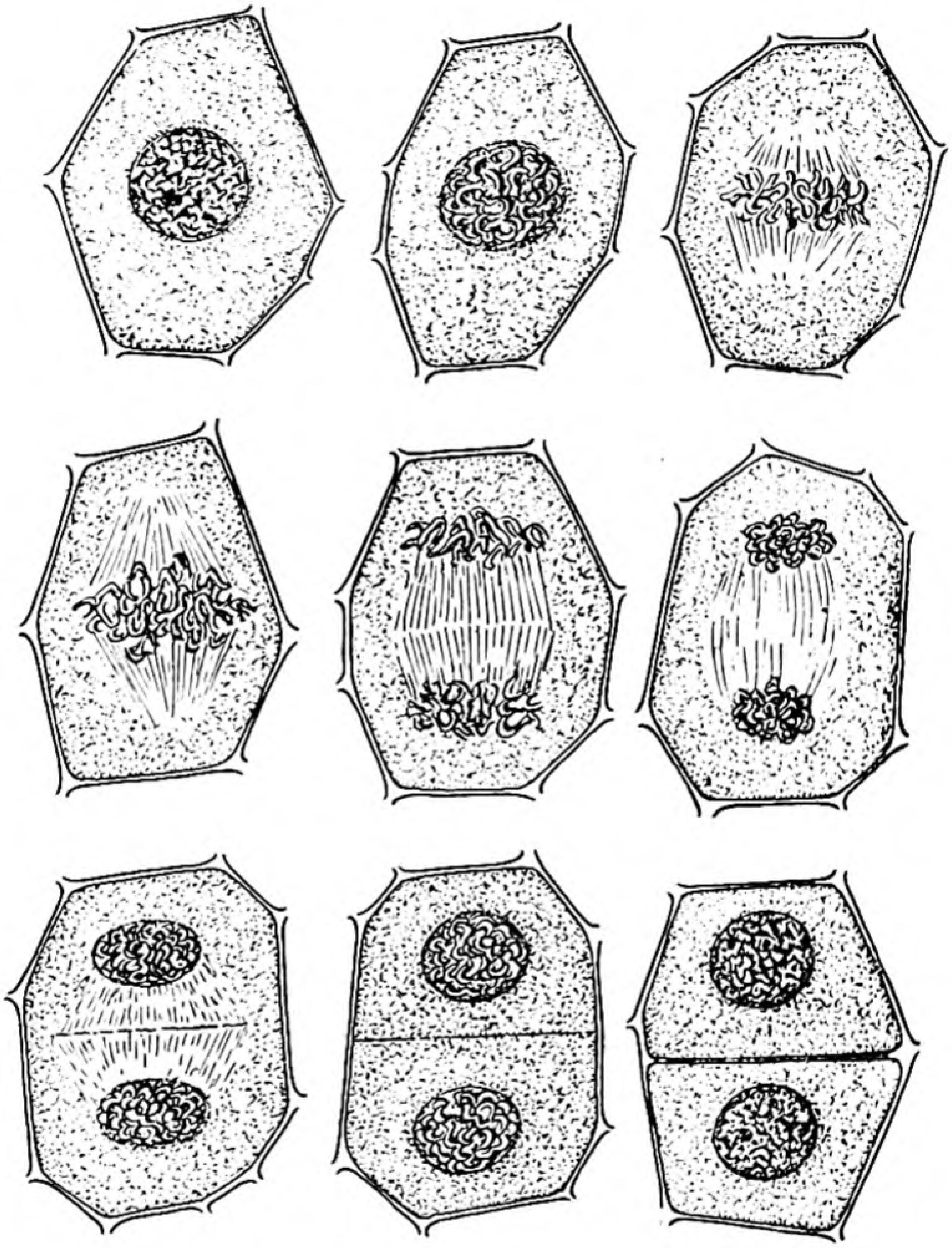


Fig. 15. Stages in Mitosis and Cell Division.

9. The Cell-Plate

During the telophase there is developed across the equatorial region of the mother cell a delicate " membrane " or cell-plate. It has been suggested recently that this cell-plate begins as a series of minute droplets which coalesce to form a fluid layer, and that plasma membranes form at the protoplasmic surfaces in contact with this layer. In this region the spindle persists longest, and spreads laterally until it reaches the lateral walls of the mother cell.

By some means, which is still rather obscure, the cell-plate gives rise to the *middle lamella*. Where this touches the wall of the mother cell it effects a junction. There is reason to believe that the middle lamella is at least double in structure, so that when it joins up with the wall of the mother cell, each daughter cell has its own distinct membrane. Later, as the daughter cells mature, they may round off by partial separation of their respective walls, leaving intercellular spaces between them. These spaces are important for aeration, as we shall see later.

The middle lamella is usually considered to consist of *pectic compounds*, and on this further layers of material are deposited. The pectic compounds may be pectin or calcium pectate (an insoluble salt of pectic acid). In many fruits insoluble pectin compounds are broken down as the fruit ripens, forming water-soluble compounds which can be readily extracted from ripe fruits such as gooseberries and apples. These pectic compounds are the cause of the gelatinisation which takes place in fruit jelly making.

10. The Cell-Wall

Very soon after cell division, layers of cellulose, and possibly some pectin, are deposited on either side of the middle lamella. During this early phase of wall formation, the cell-wall, although undergoing thickening, remains capable of extension, and so the cell can, and generally does, enlarge. Gradually, a secondary wall, consisting usually of layers of cellulose, is laid down, and as this process continues, the walls lose their power of growth, although they retain a considerable degree of elasticity, and can be stretched or otherwise deformed, without suffering any permanent change in size or shape.

In young cells, therefore, the cell-wall consists mainly of cellulose deposited on a middle lamella of pectin compounds. The cellulose is a carbohydrate which, under suitable treatment, will break down to give glucose. Recent work has shown that the cellulose molecule consists of a chain of glucose molecules, united together with the elimination of water. Each cellulose molecule consists of about 200 glucose groups, and the cellulose molecules are aggregated into groups of about 60. It is from these bundles of cellulose molecules that the cell-wall is built up. These groups of cellulose molecules are often spoken of as micella, and in the cell-wall there are spaces between the micella, known as inter-micellar spaces. The micella are colloidal in nature and in a young cell are saturated with water, whilst water, or an aqueous solution, fills the inter-micellar spaces. Water and dissolved substances will pass freely through this cellulose wall, and hence any liquid in which the cell is bathed is able to diffuse through the cell-wall and come into intimate contact with the cytoplasm of the cell.

Later, further thickening of the cell-wall may occur, due either to deposits of cellulose or to the deposition on, or impregnation of, the cell-wall with other substances, bringing about important changes in its properties.

11. Thickening and Alteration of the Cell-Wall

We have already seen that in the young cell the cell-wall is thin and composed mainly of cellulose deposited on a middle lamella, probably consisting of calcium pectate. As the cell increases in size, usually by vacuolation, fresh cellulose, built up by the activity of the living protoplasm, may be incorporated in the cell-wall in two ways: *intussusception*, where the new cellulose particles are deposited between those of the existing cell-wall so that the latter grows in area; and *apposition*, in which the cellulose particles are laid down on the surface of the original wall, by which means the latter is thickened. It is probable that both methods may go on simultaneously, the former predominating during active enlargement of the cell, the latter when the cell-wall is increasing in thickness.

The thickened cell-wall will have the same composition as the young cell-wall, and will possess the same or very similar physical and chemical properties, but often, besides being thickened, the cell-wall becomes altered by impregnation with substances other than cellulose. It may be cutinised (see § 14), lignified (see § 16), become mucilaginous, or be impregnated with mineral matter such as silica.

12. Hemicelluloses

On the original cellulose cell-wall we may get deposited hemicelluloses. Whereas cellulose is built up from glucose molecules, hemicellulose (sometimes called reserve cellulose) is built up from glucose and the molecules of other sugars such as fructose, galactose and mannose. Hemicelluloses are deposited on the cell-walls especially in some seeds, e.g. nux vomica, lupin, date and coffee, where they represent reserve food-materials which will be used when the seed germinates. During the growth of such cell-walls the cytoplasm maintains intimate contact with the surface of the cell-wall, and also through its thickness, by means of delicate threads, which form protoplasmic connexions between contiguous cells. These *plasmodesma* can be demonstrated, e.g. in the collenchyma of cherry-laurel leaves, in the thick-walled cells of the endosperm of nux vomica, where they are more or less evenly distributed, and of date-stones, where they are limited to pits.

13. Cuticularisation

Cuticularisation is due to the formation of a waxy substance called **cutin**, which forms a continuous layer, called the **cuticle**, over the external walls of epidermal cells. The cuticle is probably

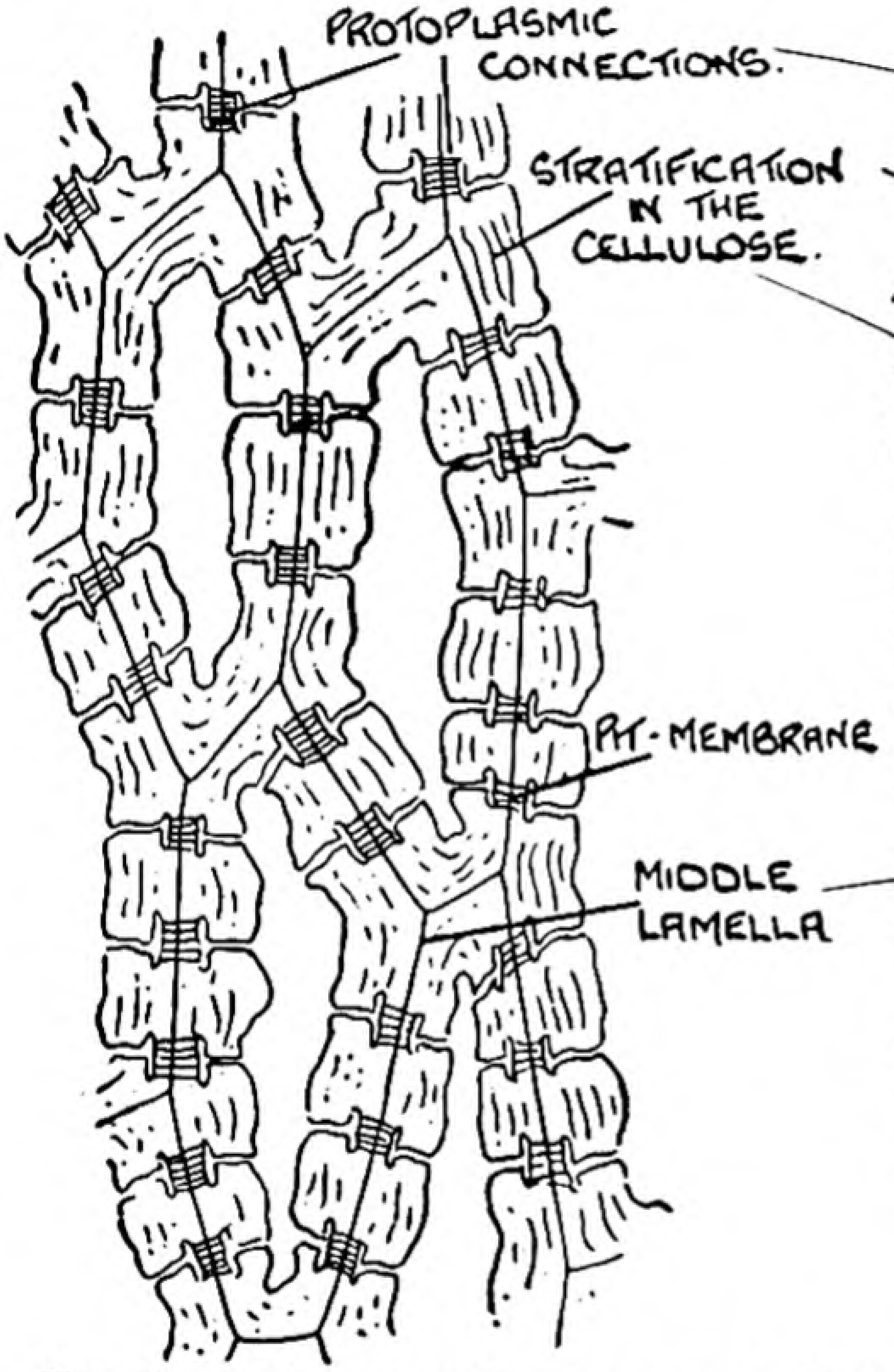


Fig. 16, A. CELLS OF ENDOSPERM OF DATE. Semidiagrammatic section to show thickened cellulose walls and characteristic pits.

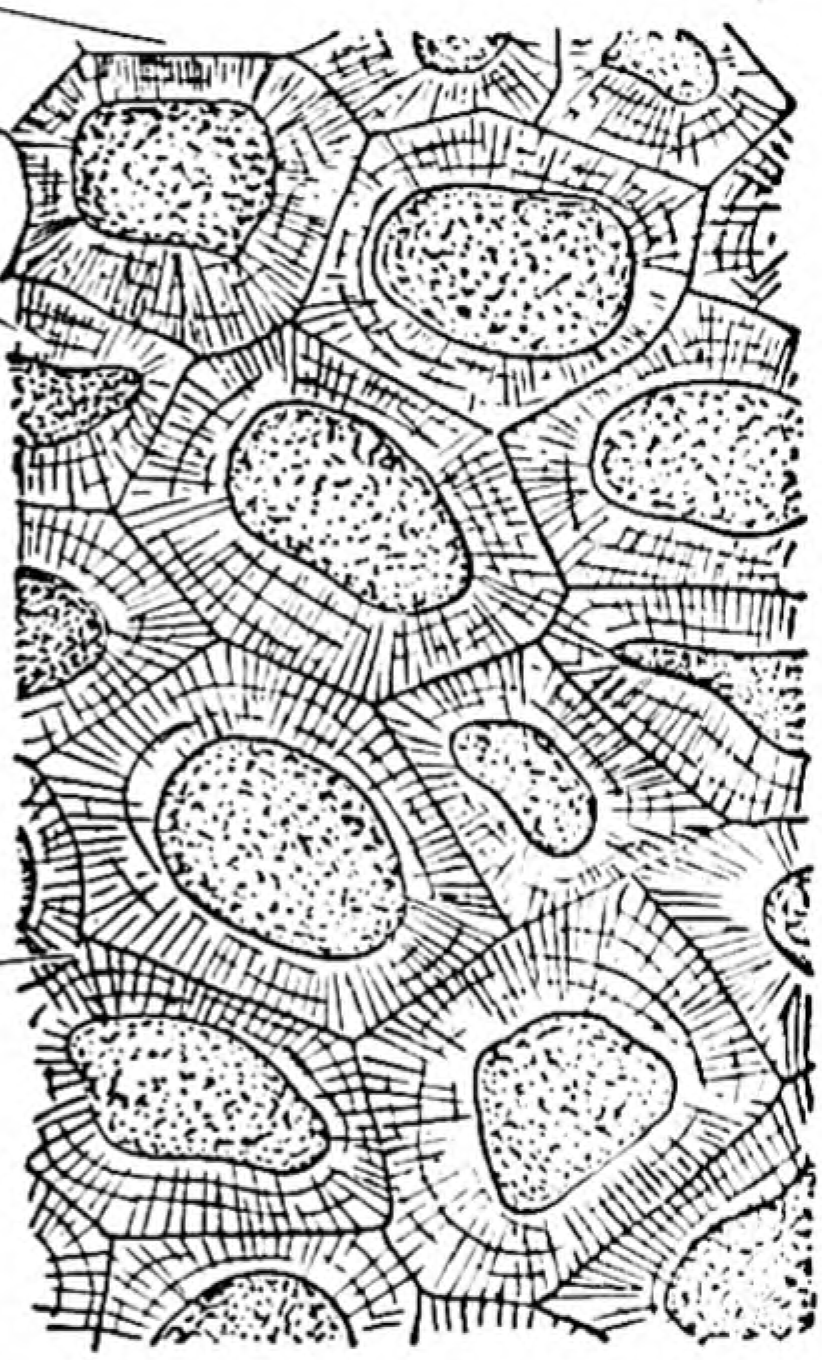


Fig. 16, B. CELLS OF NUX-VOMICA ENDOSPERM TO SHOW PLASMODESMA.

secreted through the epidermal cell-wall by the activity of the living protoplasm. It is almost impermeable to water, and hence helps to protect the cells below it from excessive loss of water. It also gives firmness to the cell-walls. The cuticle varies in thickness, being thicker in plants which grow in dry, sunny situations; its surface may be smooth, giving the glossy appearance to leaves, as in many evergreens, and to fruits, such as apples and tomatoes,

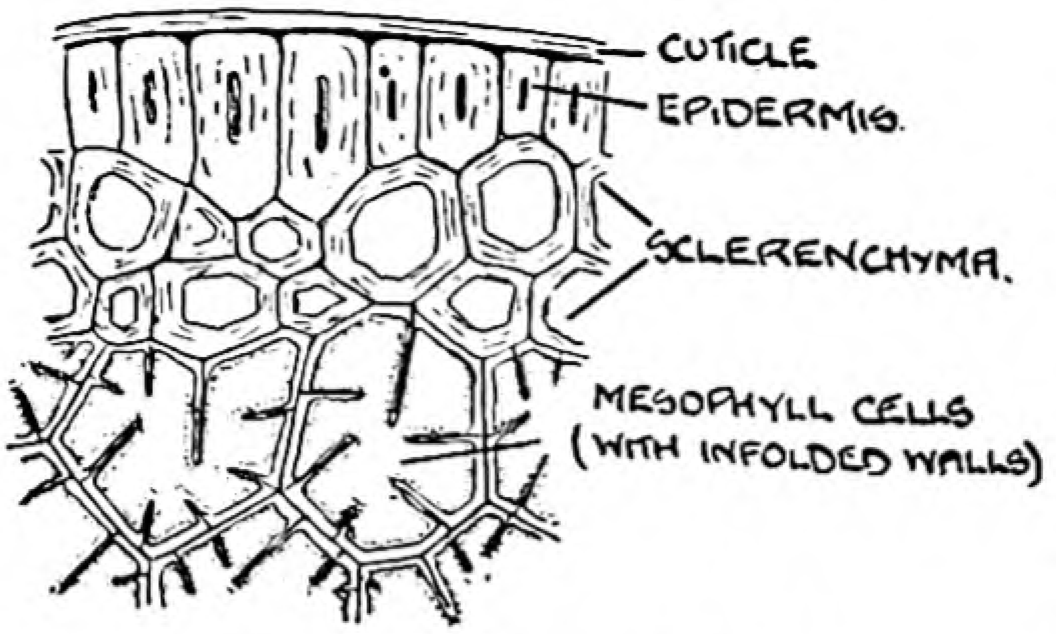


Fig. 17. LEAF OF *Pinus*.

Cuticularised epidermis, hypodermis of sclerenchyma, mesophyll of parenchyma with infolded walls.

or it may be slightly ridged, appearing finely striated under the microscope, as in leaves of *Atropa Belladonna.*

Cutin may also impregnate the cell-wall, in which case it may affect the outer walls, but sometimes the lateral walls, of the epidermis.

14. Wax

Covering the cuticle there may be a layer of wax, giving a matt or glaucous surface, e.g. to leaves, and forming the "bloom" of fruits such as grapes and plums. Occasionally the wax layer is quite thick, as on the leaves of the wax palm (*Copernicia*), and can be utilised commercially as vegetable wax.

15. Suberisation

This is due to the formation of a fat-like substance called **suberin.** Cork cells have suberised walls. It is the middle layer of the cell-wall which is suberised, and thus rendered almost impermeable to water.

Cutin and suberin are stained yellow by iodine solution, and yellow or brown by Schulze's solution. They are not acted on by sulphuric acid.

16. Lignification

Lignification is due to the deposition in the cell-wall of a number of substances collectively known as **lignin,** which become intimately mixed with both the middle lamella and cellulose layers of the cell-wall.

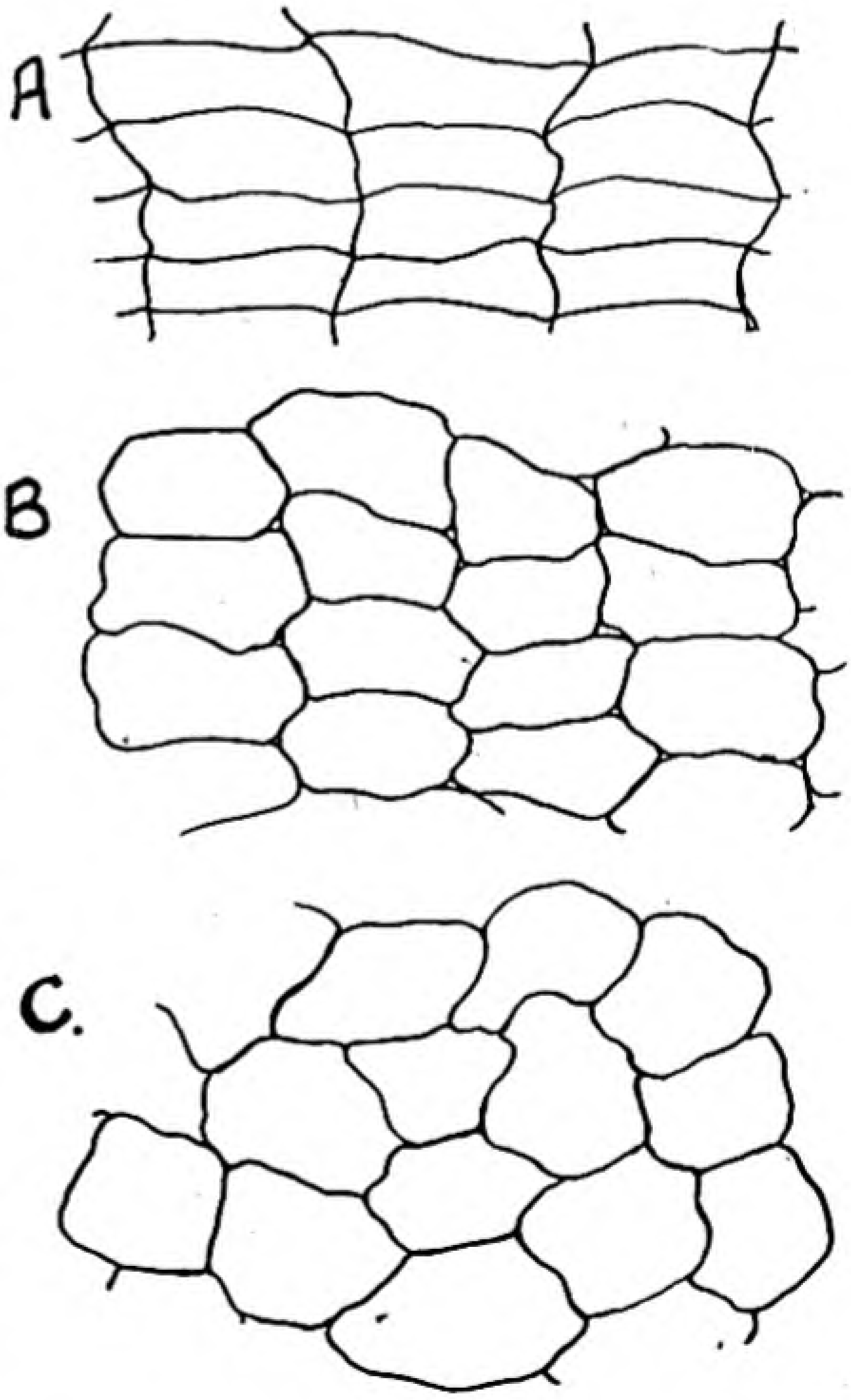


Fig. 18. CORK CELLS.

A, Transverse; B, Radial and C, Tangential Sections.

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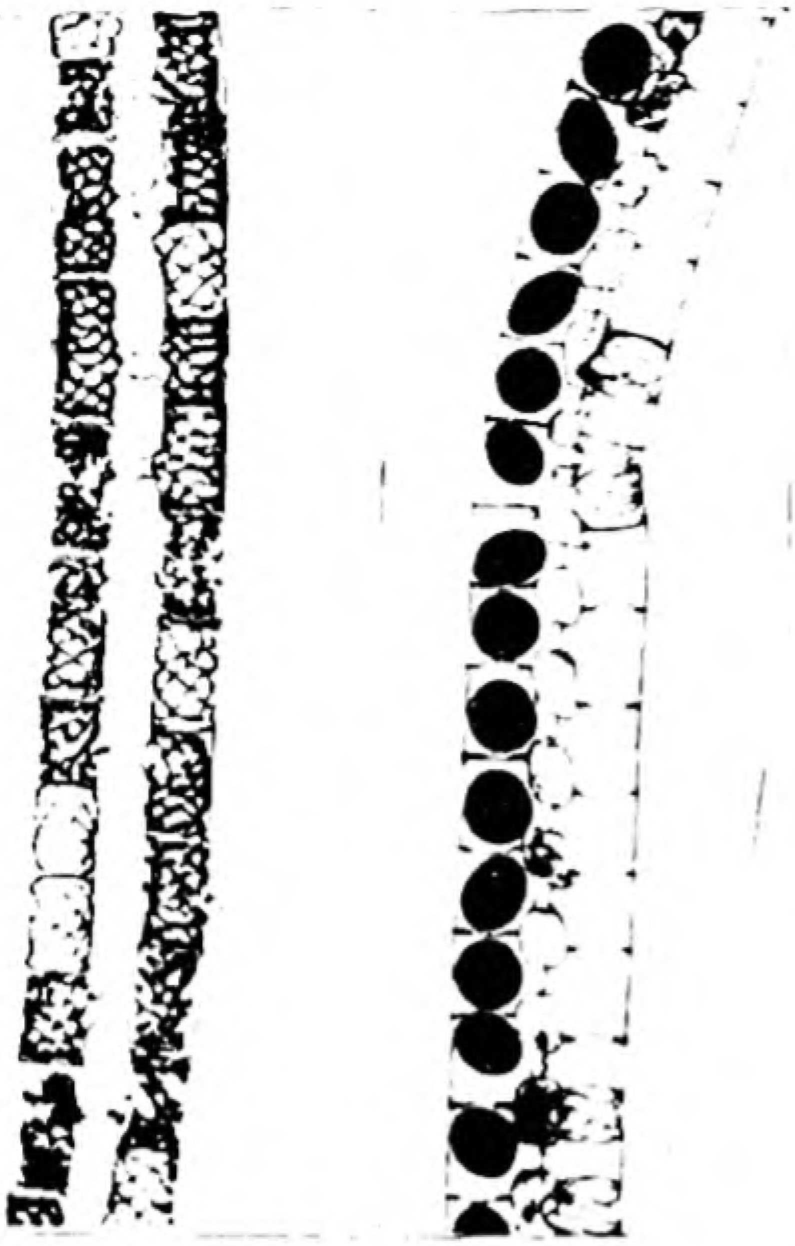
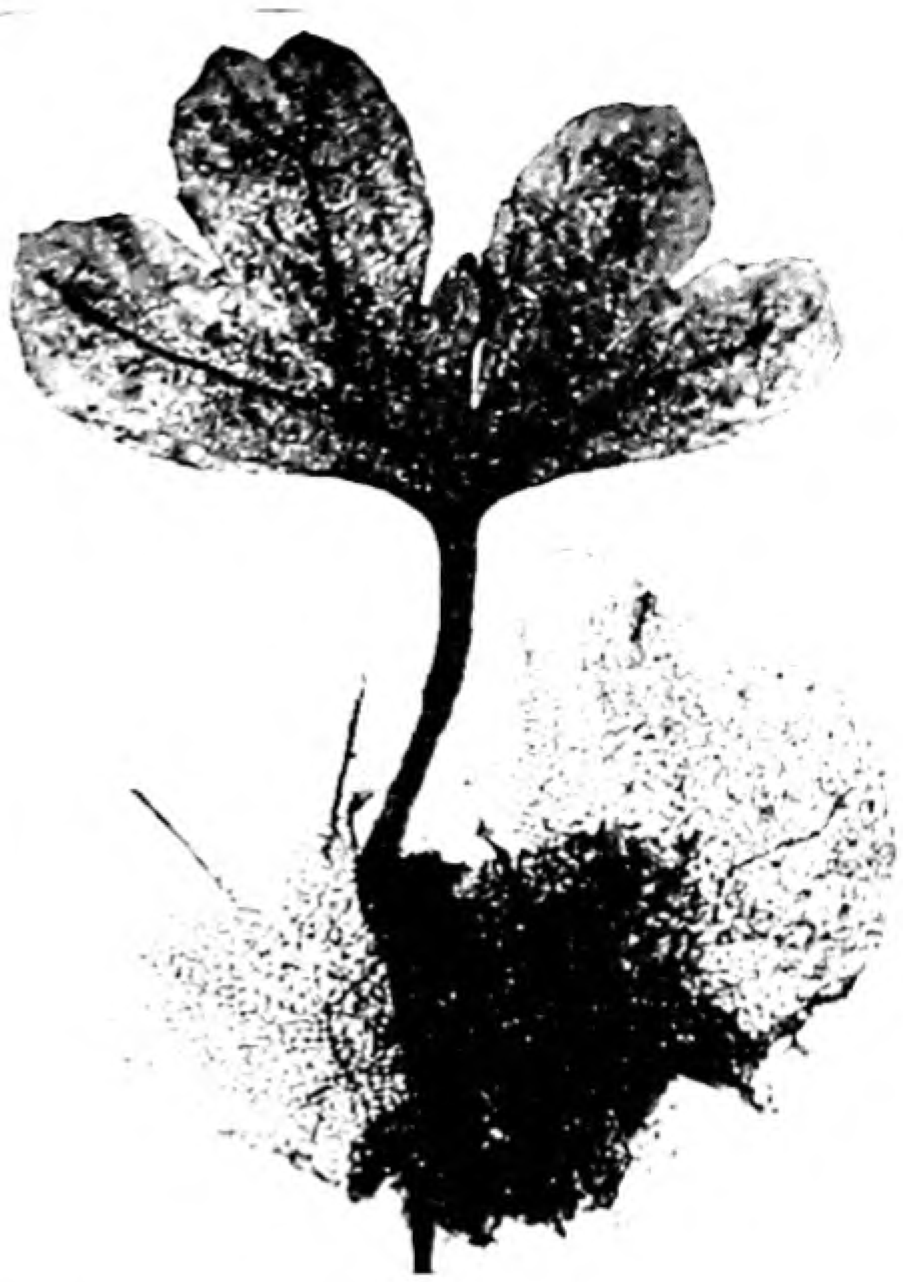




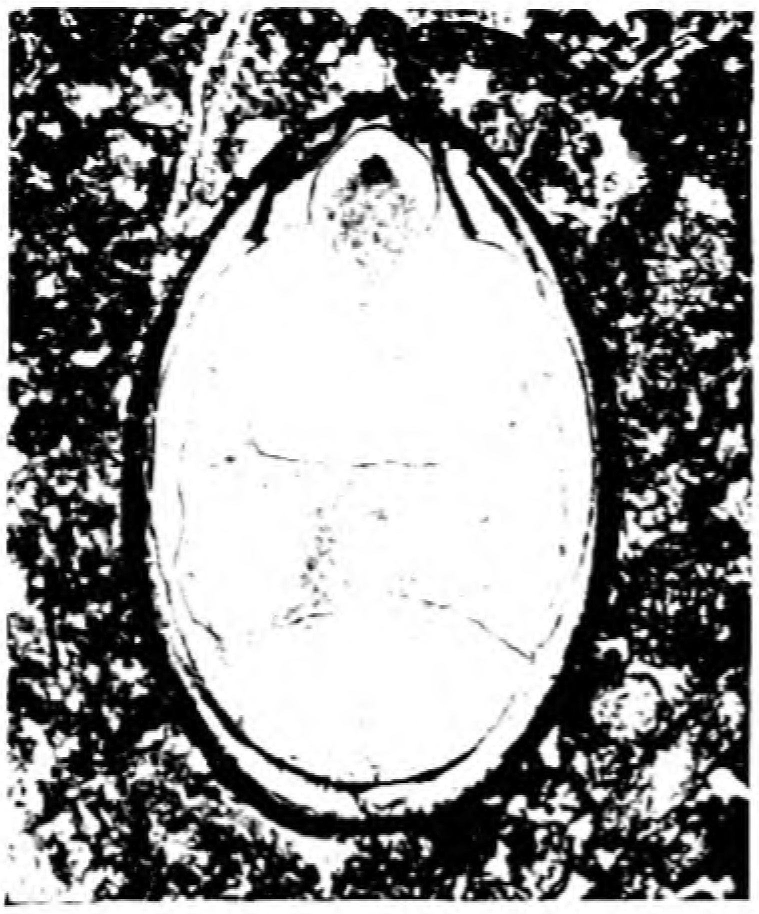
2

3

All photos: Flatters & Garnett.

PLATE I

1. Conjugation in *Spirogyra*, early and late stages.
2. Young Sporophyte of Fern attached to Prothallus.
3. A group of Toadstool Fungi.



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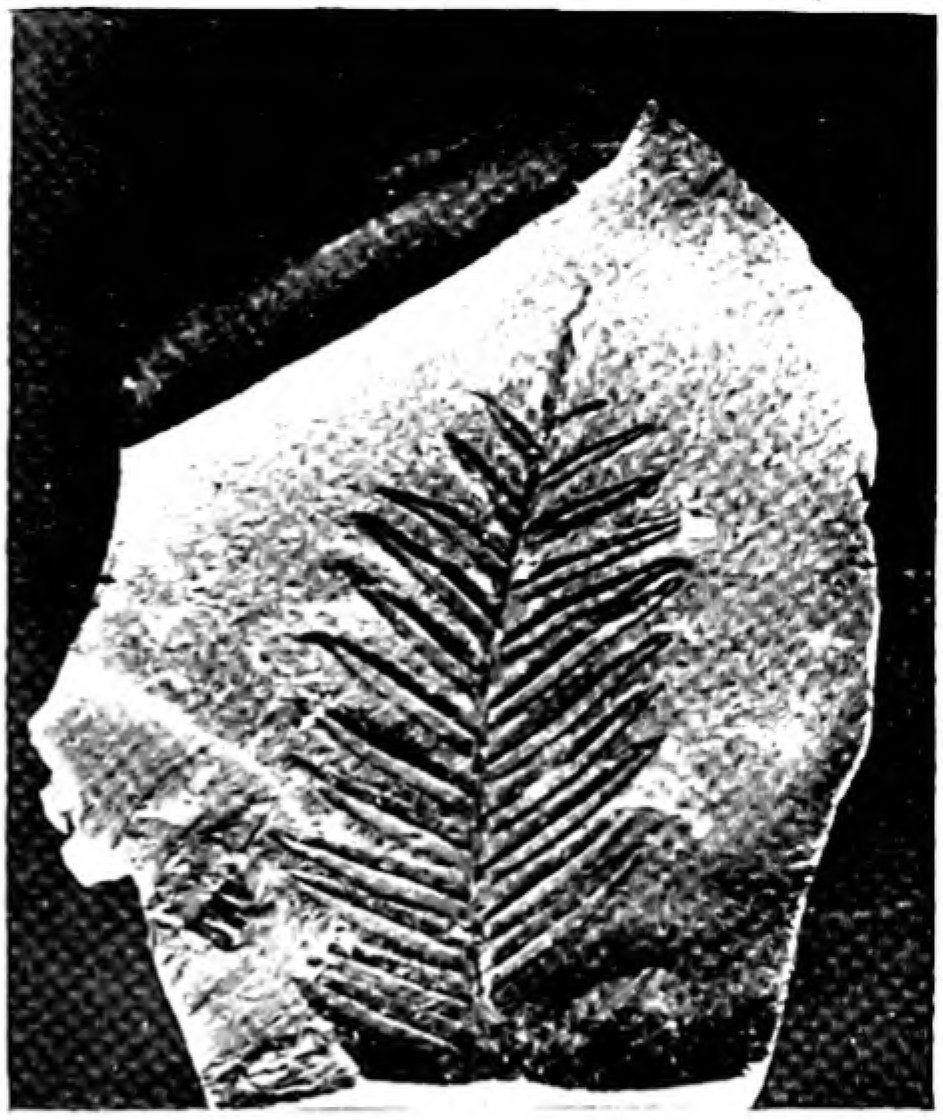

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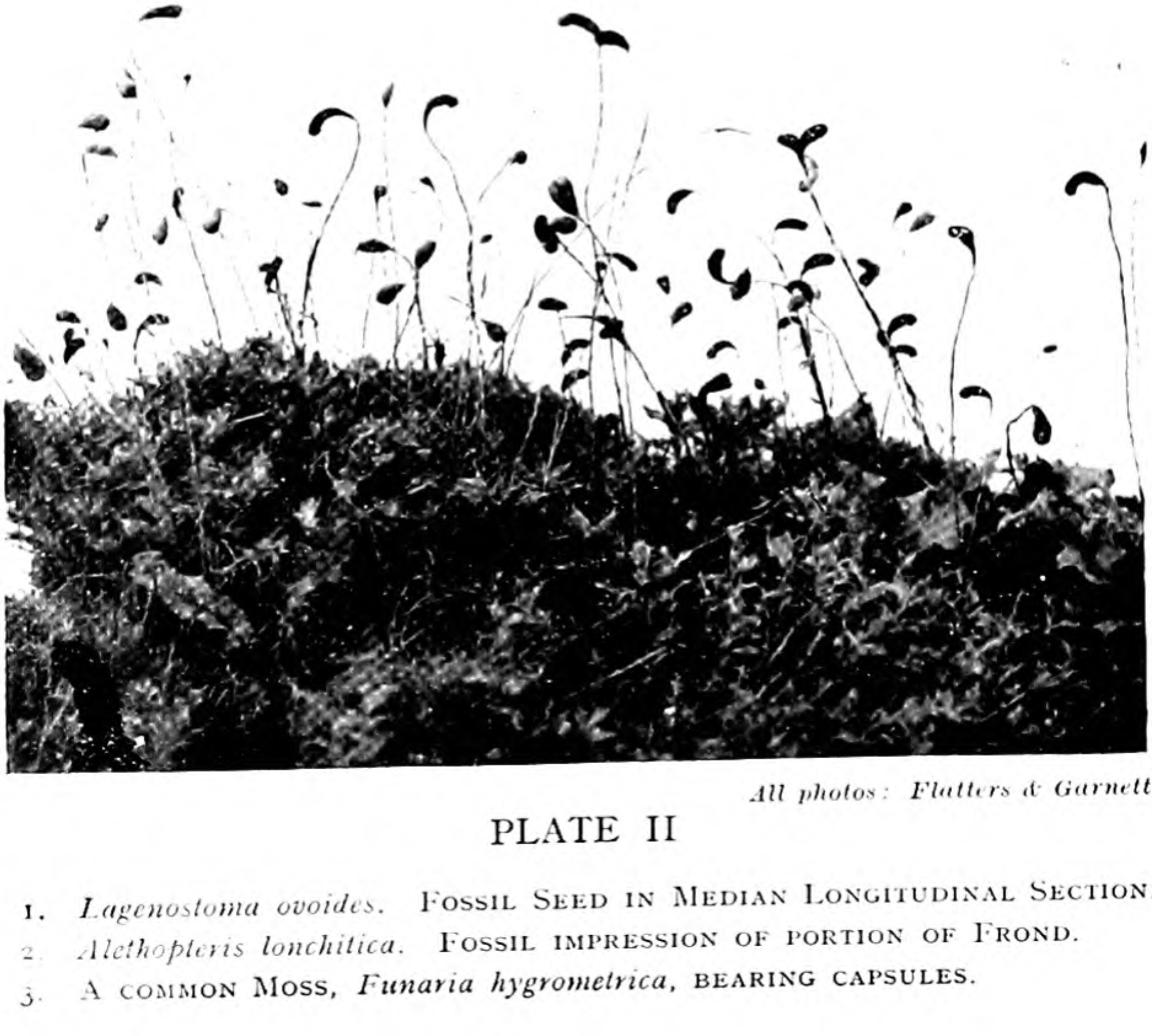

3

All photos: Flatters & Garnett.

PLATE II

1. *Lagenostoma ovoides.* Fossil Seed in Median Longitudinal Section.
2. *Alethopteris lonchitica.* Fossil impression of portion of Frond.
3. A common Moss, *Funaria hygrometrica,* bearing capsules.

The mode of origin of the lignin is obscure, but lignification of the cell-wall is usually accompanied, or followed, by the death of the protoplasm in the cell. Hence cells with lignified walls are generally dead. Lignification confers increased strength and rigidity on the cell-wall, and at the same time reduces its elasticity. It leads to profound changes in the chemical reactions of the wall which, if impregnated with lignin, is stained a bright yellow with aniline sulphate or chloride, yellow or brown with iodine, yellow with Schulze's solution, and bright red with phloroglucin and hydrochloric acid.

Delignification can be accomplished by prolonged boiling of lignified tissues, e.g. wood, in solutions of calcium bisulphite or caustic soda under pressure, or by alternate treatment with chlorine and sodium hydroxide. The cellulose wall remains. Cellulose wadding is delignified gymnospermous wood.

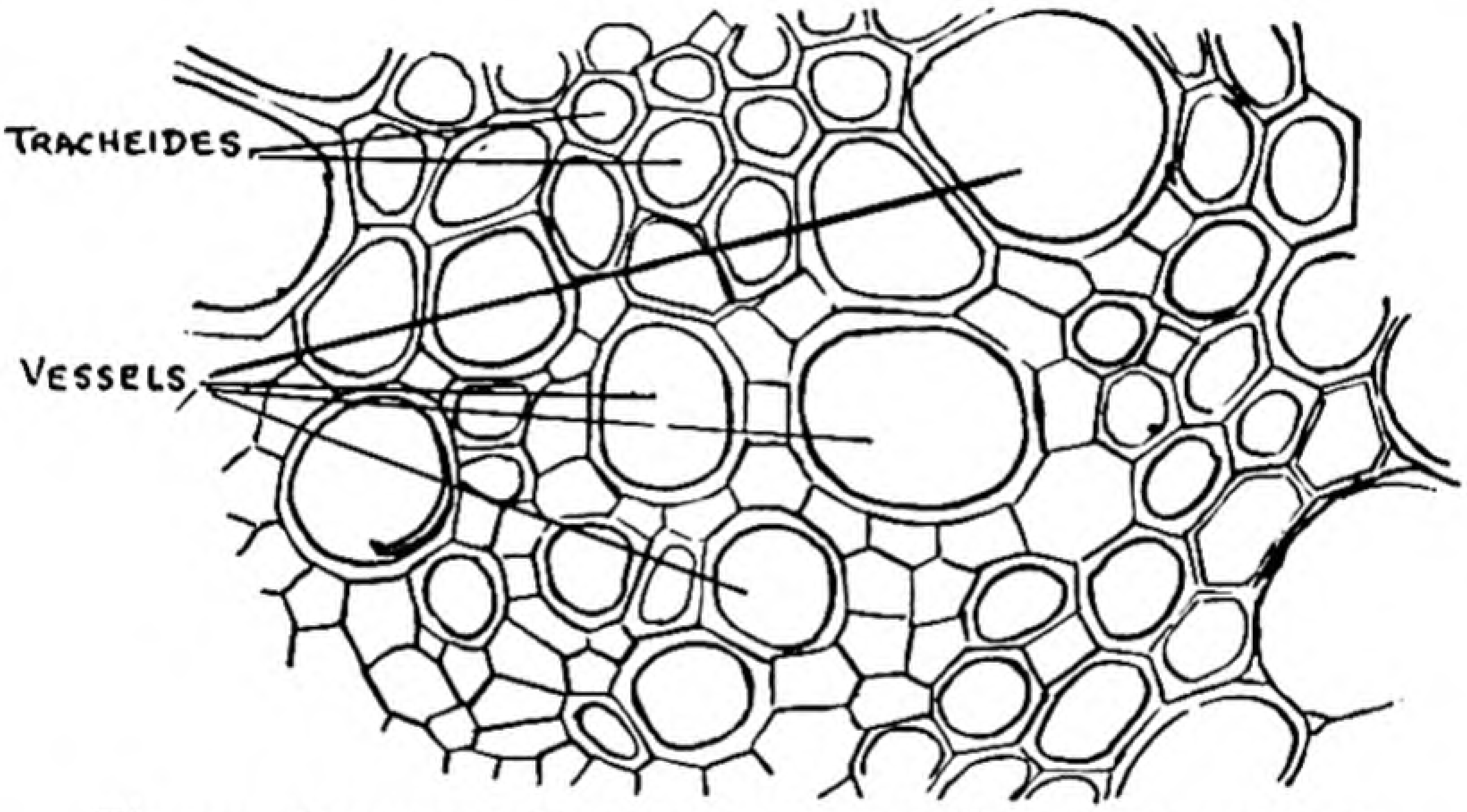

Fig. 19. LIGNIFIED ELEMENTS OF THE XYLEM AS SEEN IN TRANSVERSE SECTION.

17. Mucilaginous Cell-walls

When dry, these are hard and horny, but when moistened they absorb water, soften and swell up. The cell-walls of seaweeds are generally mucilaginous, hence their slimy character. Mucilaginous cell-walls are found in the seed coats of many seeds, and in the specialised mucilage cells found in certain plants such as slippery elm bark (*Ulmus fulva*), and marshmallow root (*Althaea officinalis*).

Chemically the mucilages are regarded as substances formed by the union of many and diverse sugars (e.g. glucose, arabinose, xylose, etc.), together with complex acidic substances. Similar to mucilages in composition are *gums*, which often result from an alteration of the cell-wall, either naturally or as the result of injury. The process is known as gummosis, and results in the complete loss of cellular structure. Tragacanth exudes from the stems of *Astragalus gummifer* when they are incised, and Gum Arabic from species of *Acacia*, especially induced by wounding. Both plants are members of the family Leguminosae.

18. Mineral Substances

Mineral substances are sometimes deposited in cell-walls. High percentages of *silica* are found impregnating the walls of the epidermal cells of grasses, sedges, horsetails (*Equisetum*), etc., sometimes so completely that, if the tissue is burned, a complete siliceous skeleton of the cells is left behind. This impregnation of the cell-wall may help to confer rigidity on the tissues and possibly afford protection against small animals. Certain small marine plants (diatoms) have a siliceous wall. A number of marine Algae, and a few freshwater plants have a cell-wall which becomes encrusted with *calcium carbonate*, whilst isolated crystals of calcium oxalate, and, less frequently, of calcium carbonate, may occur in the cell-walls of certain land plants.

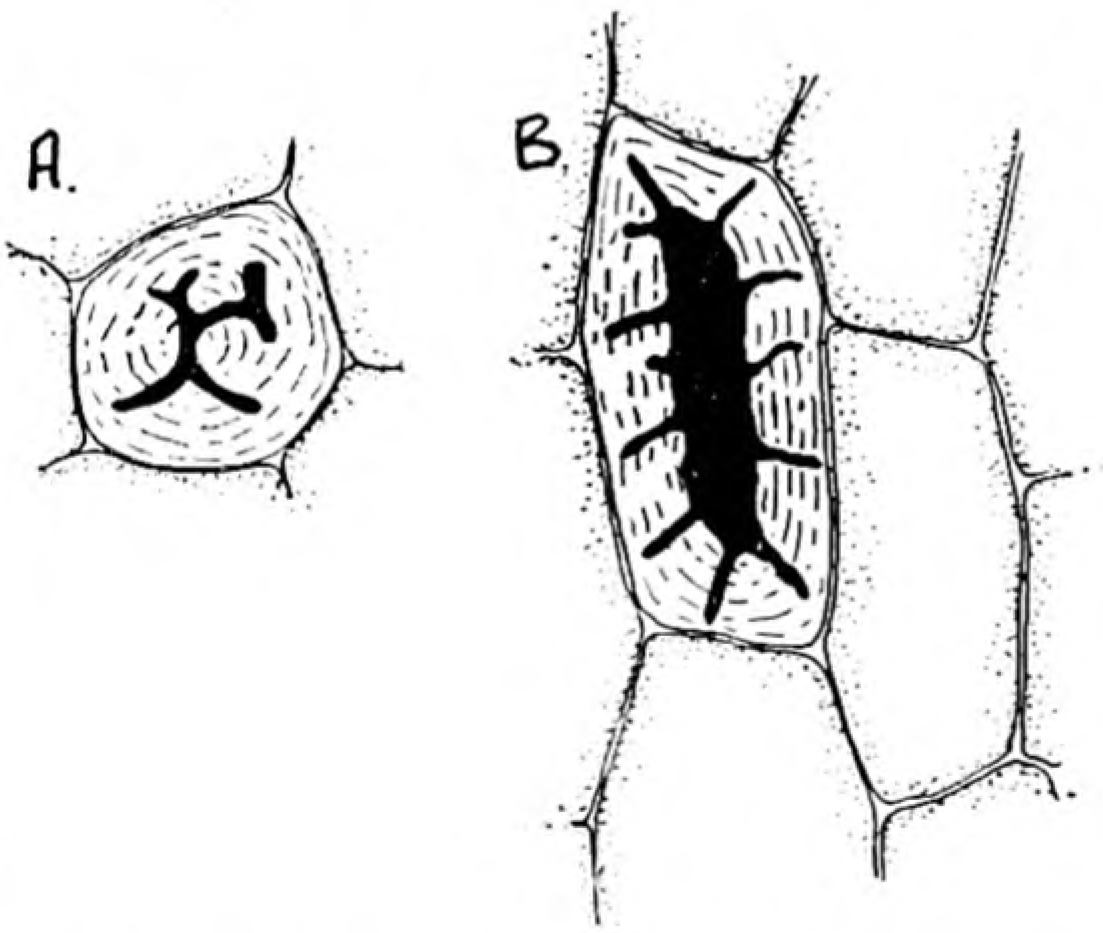

Fig. 20. Mucilaginous Cell-walls in Phloem of *Ulmus fulva*.

B. The Tissues

A **tissue** may be defined as an aggregation of similar cells or elements, united from the first, governed by the same laws of growth and development, having therefore a similar structure and performing the same function. The significance of the differentiation of tissues has already been indicated. The tissues of a plant may be arranged in two chief groups: (*a*) **Meristematic Tissues** ; (*b*) **Permanent Tissues.** The former are found e.g. at growing points. They consist of meristematic cells, *i.e.* cells which possess the power of dividing. In the latter group are included all tissues derived from the former by various processes of differentiation. They consist of cells or elements which have lost the meristematic property, and taken on some fixed or permanent structure, and which perform some special function.

19. Meristematic Tissues

As already indicated (§ 2), the regions of meristem may be restricted, as at the apices of stems and roots (**apical meristems**) where they provide further growth in length. But frequently growth in length may also take place through meristematic activity persisting behind the growing point in regions separated by permanent tissues. Such meristematic zones are said to be **intercalary.** Both types of meristem illustrated above are also **primary,** because the cells have retained their activity throughout the life of the organ in which they are situated. But living cells of permanent tissue may take on meristematic activity, either in the course of normal growth in thickness, as in woody stems and roots, or as a result of injury. Such meristems are **secondary.**

The structural characters of meristematic cells have already been described (§ 2 *et seq.*). They may differ in form, according to their position in the plant, but in structure they are similar in that they possess a thin cell-wall which encloses a protoplast consisting of cytoplasm and a large, well-defined nucleus. There are no intercellular spaces.

20. Permanent Tissues

As the cells arising by the activity of meristematic cells become progressively older, a gradual differentiation takes place. This is observed readily in longitudinal sections of a root-tip. Behind the region of active cell division, the cells enlarge and vacuoles appear. Vacuolated cells make up a large part of the permanent tissue of plants (see parenchyma, below), but further differentiation takes place in some cells, or groups of cells, by changes in form, size, character of cell-wall and contents. The early phases of differentiation may be recognised in some plants in the meristematic region by a more or less distinct arrangement of three zones, called **histogens,** *viz.* an outer limiting layer of cells, the **dermatogen,** a central cylinder of cells, the **plerome,** and, between these two, the **periblem,** of several layers of cells. The root-tip differs from the stem-tip in possessing a fourth histogen, the **calyptrogen,** forward of the apical meristem, which gives rise to the root-cap (see Chap. V, § 7). Often there is no distinction between periblem and plerome. Tracing development from the apex backwards we find that some cells retain their meristematic character longer than others, and that still further back, whilst some cells are still elongating by vacuolation, others are already past this stage. This is particularly noticeable in those groups of cells, called **desmogen** strands, which eventually differentiate completely into conducting tissues known as vascular bundles. In these strands the maturation of specialised conducting elements has commenced on the inner and outer sides whilst contiguous cells are still vacuolating (see protoxylem, page 43, § 26).

The classification of permanent tissues given below is based on the characters of wall and contents of the component elements of these tissues. In describing these characters, mature cells are chosen, but it must be borne in mind that there may be intermediate or transitional forms, so that the demarcation between one tissue and another need not necessarily be as clearly defined as the description suggests.

21. (1) Parenchyma

This (see Fig. 21) is one of the commonest kinds of tissue found in plants. It constitutes the greater part of the soft succulent tissue, e.g. the tissue of Algae and mosses, the cortex and pith of stems, the mesophyll of leaves. The cells may be round or oval, with numerous intercellular spaces (spongy parenchyma, Fig. 22), slightly elongated and arranged perpendicularly to some surface (palisade parenchyma, Fig. 22), elongated and prismatic, stellate, etc. The cell-walls are usually thin and consist of cellulose. Cytoplasm, nucleus, vacuole, and cell-sap are present. Various substances may be formed in the cells, such as starch, protein grains, oil, resin, etc. As a rule intercellular spaces are present. In the pith of some trees,

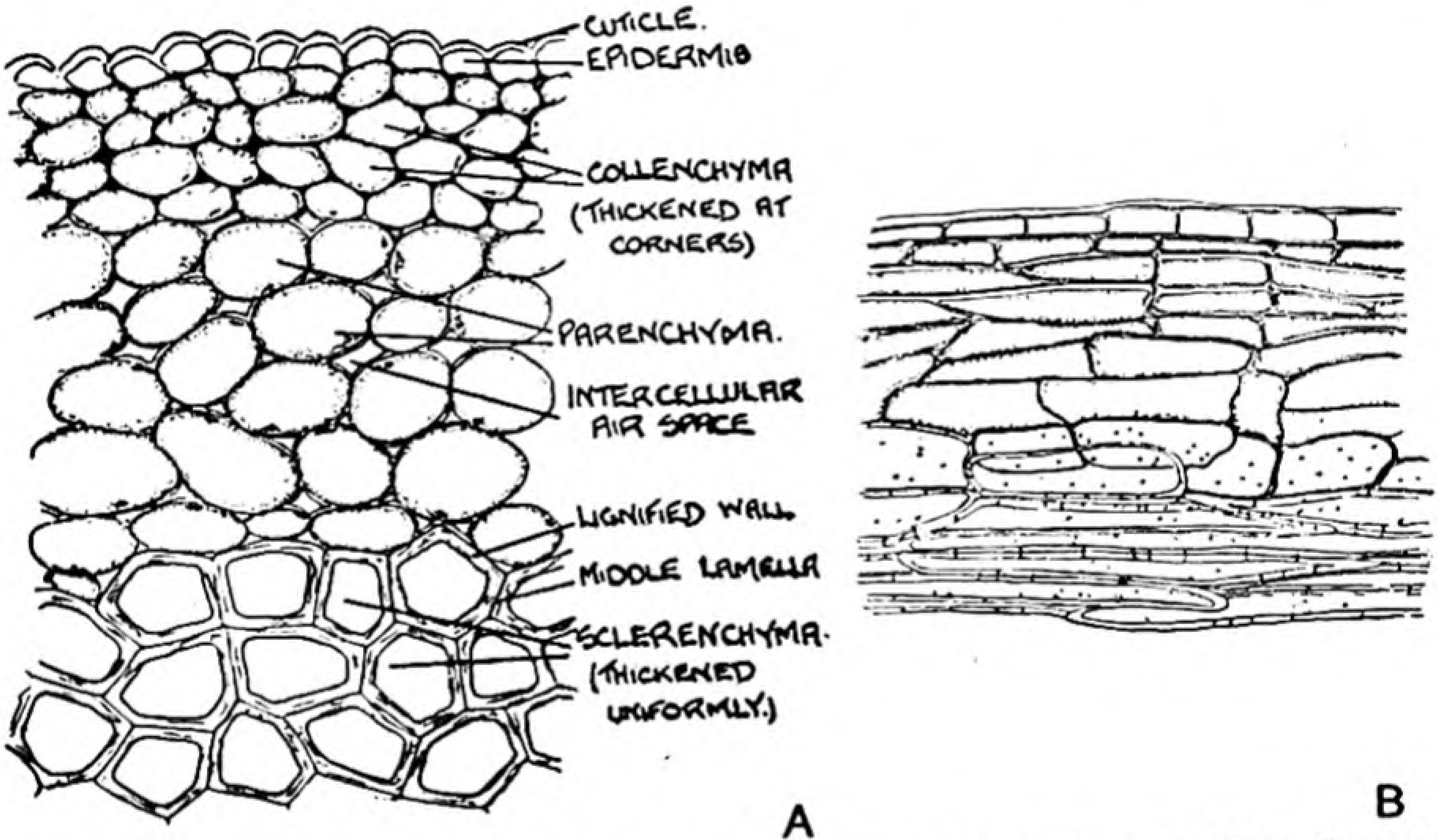

Fig. 21. A, Parenchyma, Collenchyma and Sclerenchymatous Fibres seen in Transverse Section of Midrib of *Hamamelis* Leaf; B, the same in Longitudinal Section. (Reduced scale of magnification.)

the parenchymatous cells entirely lose their contents, and the walls may become lignified.

Other types of parenchyma, e.g. xylem (or wood) parenchyma, phloem parenchyma, medullary ray parenchyma occur, and will be dealt with under their respective tissue associations.

Parenchyma is a tissue essentially engaged in the processes of nutrition. The cells containing chlorophyll can elaborate organic substances; other cells serve for the storage of these substances. Although the cell-walls are comparatively thin, parenchyma also exercises a strengthening or supporting function by reason of the turgid condition of the cells. The important part it plays in this respect is shown by the drooping of herbaceous plants when deprived of water.

22. (2) Collenchyma

In this tissue, found underneath the epidermis of many stems, leaf-stalks and midribs, the cells retain their contents, but are elongated and the cell-walls are more or less thickened. The thickened walls consist of cellulose, which is laid down more especially at the angles of the cells in longitudinal strips, or over the periclinal (tangential) walls.

The cells of collenchyma may contain chloroplasts; but in addition to nutritive functions, this tissue has a mechanical function, giving strength to the parts in which it occurs. Collenchyma is capable of elongation and is usually formed in organs which are still growing.

23. (3) Sclerenchyma

Just as there is no definite line of demarcation between parenchyma and collenchyma, so there are transitional forms between these two and sclerenchyma. Here the contents of the cells, in most cases, have been completely lost, and the walls of the elements so thickened that the cell cavities are frequently almost obliterated. The function of sclerenchyma is purely mechanical. Along with the xylem it is the chief strengthening tissue found in plants, forming an important part of what might be regarded as the plant skeleton, and its distribution in stems, leaves and roots bears a relation to the strains and stresses to which these organs are subjected.

Sclerenchyma mainly consists of two types of element, fibres and stone cells. The *fibres* are usually developed in bundles or layers; they may also occur singly. The individual fibres are elongated cells with pointed ends which interlock amongst the ends of other fibres of the same strand or layer. They do not necessarily pursue a longitudinal course; in some barks, e.g. lime, the strands of fibres form a meshwork when seen tangentially, and in quillaia alternating layers of fibres are arranged obliquely in opposite directions. The walls of the fibres are usually lignified, but they may be cellulose, or of varying proportions of cellulose and lignin. Flax fibres are practically unlignified; those of jute and hemp are lignified. The average length of a fibre varies between one and two millimetres, but some are considerably elongated, and on this account are valuable commodities. Flax fibres are from 20 to 40 mm. long, whilst ramie fibres (*Boehmeria*) attain the enormous length of 220 mm. In transverse section isolated fibres are more or less circular. Fibres associated in strands or layers are polygonal in transverse section, due to mutual pressure during development. There are no intercellular spaces. The thick walls show stratification, the optical differences between the strata being due to variations in water-content, and possibly also to other physical and chemical properties. Through the thickness of the cell-wall run pits, and the pits of contiguous fibres are usually

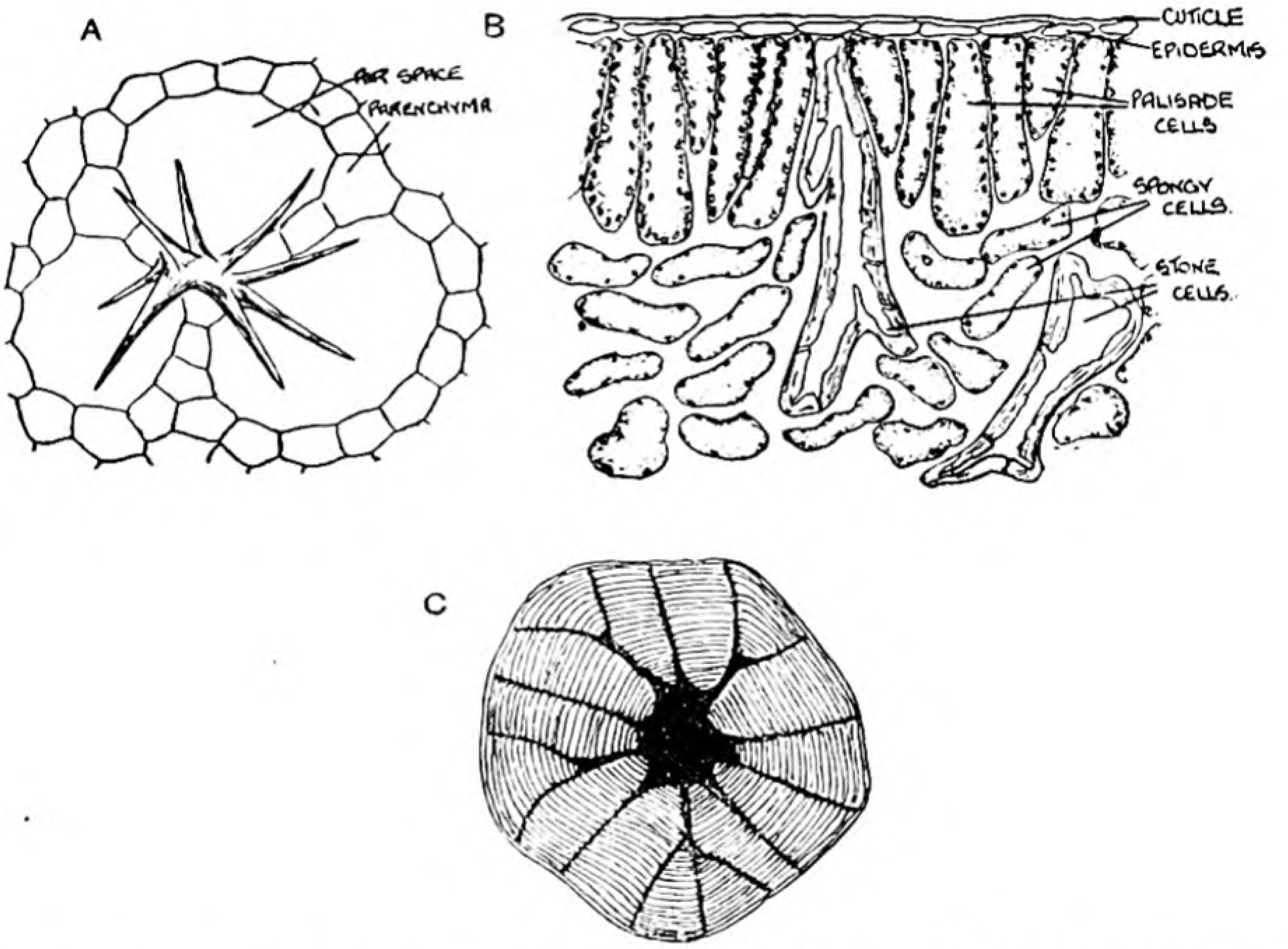

Fig. 22. A, Branched Stone-cell from Petiole of *Nymphaea*; B, Stone-cells in Leaf of *Hamamelis*, embedded amongst Palisade and Spongy Parenchyma; c, Stone-cell showing Branched Pits.

opposite to each other, each terminating at the middle lamella, which forms the pit-closing membrane common to both, so that there is no through passage, and their function in mature, dead fibres is not clear. At the middle lamella, the pit-closing membrane is usually circular, but the entrances to the pit from the cell-cavity on either side are usually slit-like and oblique in opposite directions, hence the name " cross-pits " as characteristic of sclerenchymatous fibres.

24. (4) **Stone-cells** (Fig. 22)

Stone-cells (sclerenchymatous cells) are usually more or less isodiametric, but if they are elongated their longest axis is only about four times as great as their shortest one. They may be more or less spherical, cylindrical or irregularly branched, and occur singly or in masses or layers. They occur in the flesh of succulent fruits, e.g. the "grit" in pears, and are abundant in the cortex and phloem of stems and roots and in the coverings of seeds, nuts, etc. The wall of the individual stone-cell is thick, stratified, and strongly lignified. The pits are rounded. They are numerous on the outer, middle-lamellar surface of the stone-cell, but they fuse as the thickening gradually reduces the area of the inner surface of the wall, so that in the mature stone-cell they appear as branched pits. Within the cell cavity may occur substances such as tannin, or even starch.

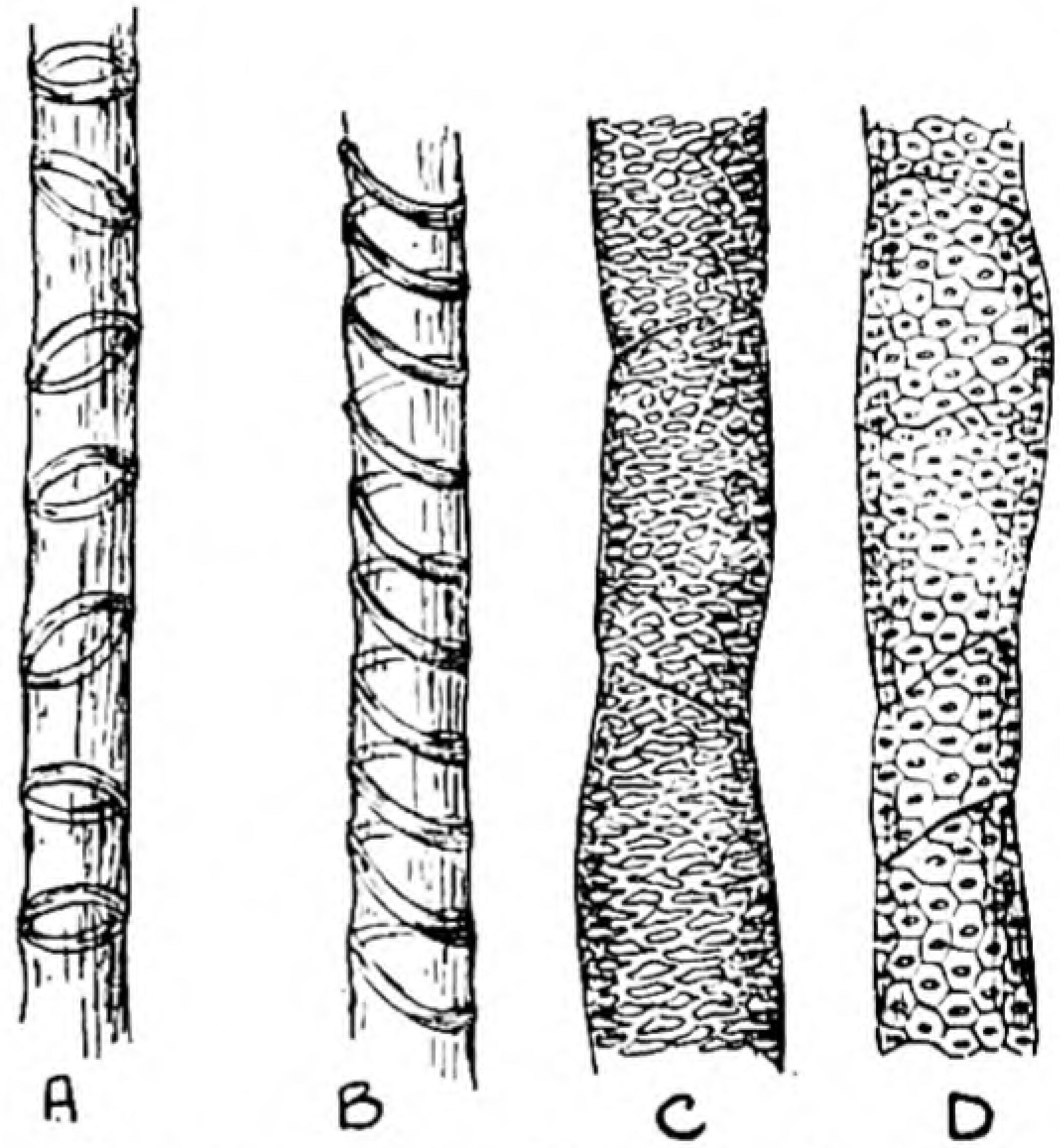

Fig. 23. XYLEM, TYPES OF VESSEL.
A, Annular; B, Spiral; C, Reticulate; D, Pitted.

25. (5) **Xylem**

This consists essentially of one or both of two kinds of elements: (*a*) **vessels** (Fig. 23); (*b*) **tracheides** (Fig. 24, A, B). In both of these the walls are thickened and usually lignified, and the protoplasmic contents have disappeared. Annular, spiral, pitted, or scalariform patterns may be developed on the walls. The tracheide, however, is developed from *a single cell*; whereas the vessel is a long, tubular structure derived by *cell-fusion* from a longitudinal row of cells.

In Angiosperms the vessels are the characteristic structures of the wood, although tracheides also are found, especially in the secondary wood of Dicotyledons. Wood vessels vary in length from a few inches to a yard, or in some cases more. In Gymnosperms and Vascular Cryptogams there are, with rare exceptions, tracheides only.

Owing to the thickening and lignification of the walls this tissue performs a mechanical or supporting function, but its special function is to carry watery solutions from the root, to the leaves and other organs.

It is not always possible to distinguish between fibres, tracheides and vessels when woody tissue composed of these elements is seen in transverse section under the microscope. Some vessels may have a wide diameter and thus stand out prominently, but others may be no wider than the tracheides or fibres. Longitudinal sections, or, better still, macerations, bring out the differences more clearly. A sclerenchymatous fibre is distinguished from a tracheide by its shape, its relatively narrow lumen and, particularly, by the character of its pits. True vessels show a double band of thickening at the junctions of the original cell membranes. The shape of the vessel is determined by the shape of the component cells, which may not necessarily have been straight or their end walls transverse. The character of the thickening varies. In some cases the lignin is laid down in the form of rings at intervals along the inner surface of the cell-wall, giving an annular vessel or tracheide (Fig. 23, A). In other cases the thickening takes the form of a spiral band, giving a spiral vessel or tracheide (Fig. 23, B), and there are intermediate forms where the thickening is partly annular and partly spiral. Such elements constitute **protoxylem,** which is the first xylem to differentiate from the primary meristems, and actually does so whilst the living cells about it are still actively dividing and elongating. The annular and spiral thickening permit of considerable extension, so that these dead elements become drawn out longitudinally as the neighbouring cells grow. The xylem of the finer veins of leaves usually consists of spiral tracheides, which can be seen when a leaf is cleared of its cell contents and rendered transparent by treatment with Eau de Javelle or chloral hydrate solution, and examined under the microscope.

As elongation slows down, the later-formed spiral elements show a closer and closer arrangement of the turns of the spiral. Then we get reticulately thickened elements where the thickening forms a network on the inner surface of the original cell-wall (Fig. 23, C).

Finally, we have the pitted type of thickening (Fig. 23, D). In this case the whole of the wall, with the exception of numerous, small circumscribed areas, undergoes thickening. When examined under the microscope in surface view the unthickened areas *appear* like perforations, apertures or dots. As in the case of sclerenchyma, however, the middle lamella forms the pit-closing membrane. Where two contiguous cells are developing into the same type of tissue element, the architecture of the pit is the same on both sides, and the cell-wall layers tend to over-arch the pit-closing membrane, making the pore or mouth of the pit of smaller area than the closing membrane. This is called a *bordered pit*, and distinguishes vessels and tracheides from sclerenchyma.

But bordered pits vary in pattern in the different large groups of plants. Thus, in the Vascular Cryptogams the pits are transversely elongated so that the thickening between them forms bars. This form of thickening is called scalariform, because the bars appear like the rungs of a ladder. In the Gymnosperms, especially the Coniferae (e.g. *Pinus*, *Cedrus*, etc.) the bordered pits are circular and arranged in a row along the radial walls of tracheides. These bordered pits are very characteristic. The pit-closing membrane has a central thickening, the torus, shaped like a bi-convex lens; the pit cavity on each side of this is dome-shaped, and the apex of each dome is open, giving access to the cell cavity of the tracheide. Seen in surface view, as in a radial longitudinal section of pine wood, under a microscope, such a bordered pit will show an outer ring representing the boundary of the pit-closing membrane, and an inner ring representing the boundary of the pore at the cell cavity. There may be an intermediate ring, the boundary of the torus. The Angiosperms possess vessels, as well as tracheides, and the bordered pits are usually smaller than those of the Gymnosperms, and more numerous, frequently being set closely together over the whole surface of the element. Vessels and tracheides of a few woody plants have what may be termed a tertiary thickening inside the secondary one, consisting of spiral bands, loosely or tightly coiled, or reticulations. These tertiary walls must not be confused with the secondary walls which give their names to spiral and reticulate elements.

Vessels and tracheides are circular or polygonal in transverse section and have a relatively wide cell cavity. They are the channels through which water is transferred rapidly from the roots, through the stems to the leaves. They do not necessarily function thus throughout the life of the plant, for in trees the heartwood has lost this function and has become a region in which by-products may accumulate, and these are responsible for the colour and usefulness

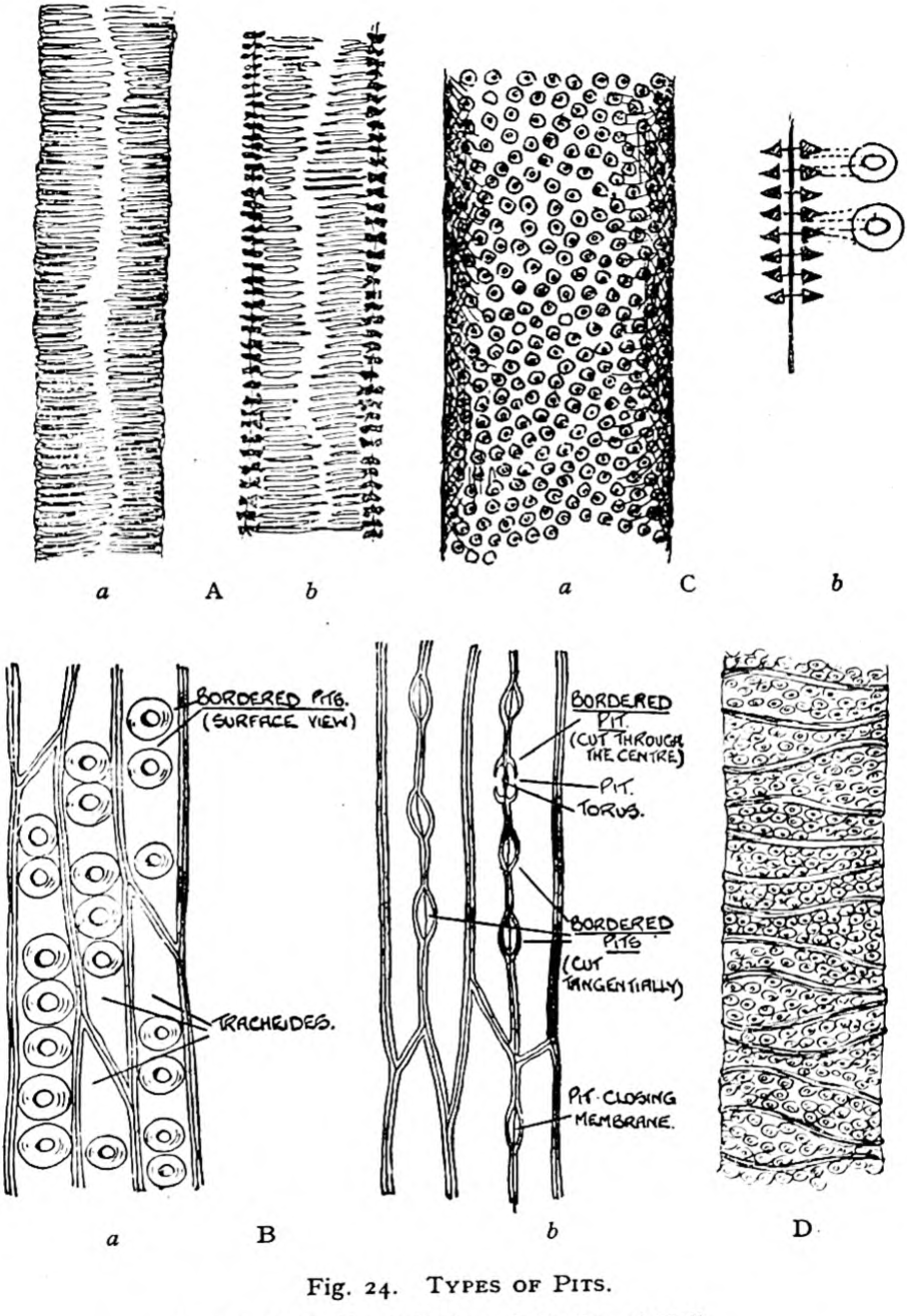
a
A
b
a
C
b
BORDERED PITS.
(SURFACE VIEW)
TRACHEIDES.
BORDERED PIT.
(CUT THROUGH THE CENTRE)
PIT.
TORUS.
BORDERED PITS
(CUT TANGENTIALLY)
PIT-CLOSING MEMBRANE.
a
B
b
D

Fig. 24. Types of Pits.

A, Fern tracheide; *a*, Surface; *b*, Section of Wall.
B, Pine tracheides; *a*, Surface; *b*, Section of Walls.
C, Dicotyledonous vessel; *a*, Surface; *b*, Section of Wall.
D, Dicotyledonous Vessel (Lime) showing also tertiary thickening of cell-wall.

of some economic woods. Such usefulness also depends on texture and relative durability, which is governed partly by the number and size of the large vessels proportionate to tracheides, and particularly to strongly lignified xylem fibres.

Xylem fibres are essentially sclerenchymatous fibres associated with the vessels and tracheides of the xylem. There are all kinds of intermediate forms between tracheides and xylem fibres, but typical fibres with thick walls and simple cross-pits occur abundantly in woody Dicotyledons. In many plants septate fibres occur, the septa of which are thin, cellulose plates which divide the cell cavity of the fibre into separate compartments.

Xylem parenchyma is also a constituent of the xylem of many Dicotyledons. It consists of vertical files of somewhat elongated cells. It is absent from the secondary wood of conifers such as pine and yew. Small xylem parenchyma cells are commonly associated with the protoxylem. These are usually thin-walled, but those of secondary wood are often thick-walled, lignified and pitted. The pits are simple, except where a cell is contiguous with a vessel or tracheide; in this case the pit is simple on the cell side and bordered on the other side. Xylem parenchyma cells are living, and store reserve materials such as starch. They are therefore readily observed in sections stained with iodine solution.

Other parenchymatous cells associated with the xylem of woody plants are the xylem or medullary rays. These are plates of cells, one or more cells thick in the middle region, more or less elongated radially and permitting of intercellular spaces between each other and the xylem elements. They are comparable with the xylem parenchyma.

26. (6) Phloem

This (Fig. 25) may consist of sieve-tubes, companion cells, phloem parenchyma, and possibly phloem fibres. **Sieve-tubes** are typically developed in the Angiosperms. In this group they are long, slender structures composed of elongated cells placed end on end. The walls are thin and consist of cellulose. The end-walls are specially thickened and modified to form **sieve-plates,** the structures characteristic of sieve-tubes. In the thickening of these end-walls small areas remain thin, forming pits. The thin membranes closing these pits are ultimately absorbed, so that the end-wall is actually perforated in a sieve-like manner, and the contiguous cells are placed in communication.

Usually the whole of the end-wall is perforated in this way to form a simple sieve-plate (Fig. 25, A). Frequently, however, when the end-wall is not horizontal, but obliquely inclined, we can recognise on it a number of areas perforated in this way, the whole structure forming a compound plate (Fig. 25, B). Less frequently in Angiosperms the sieve-plates are formed on the lateral walls.

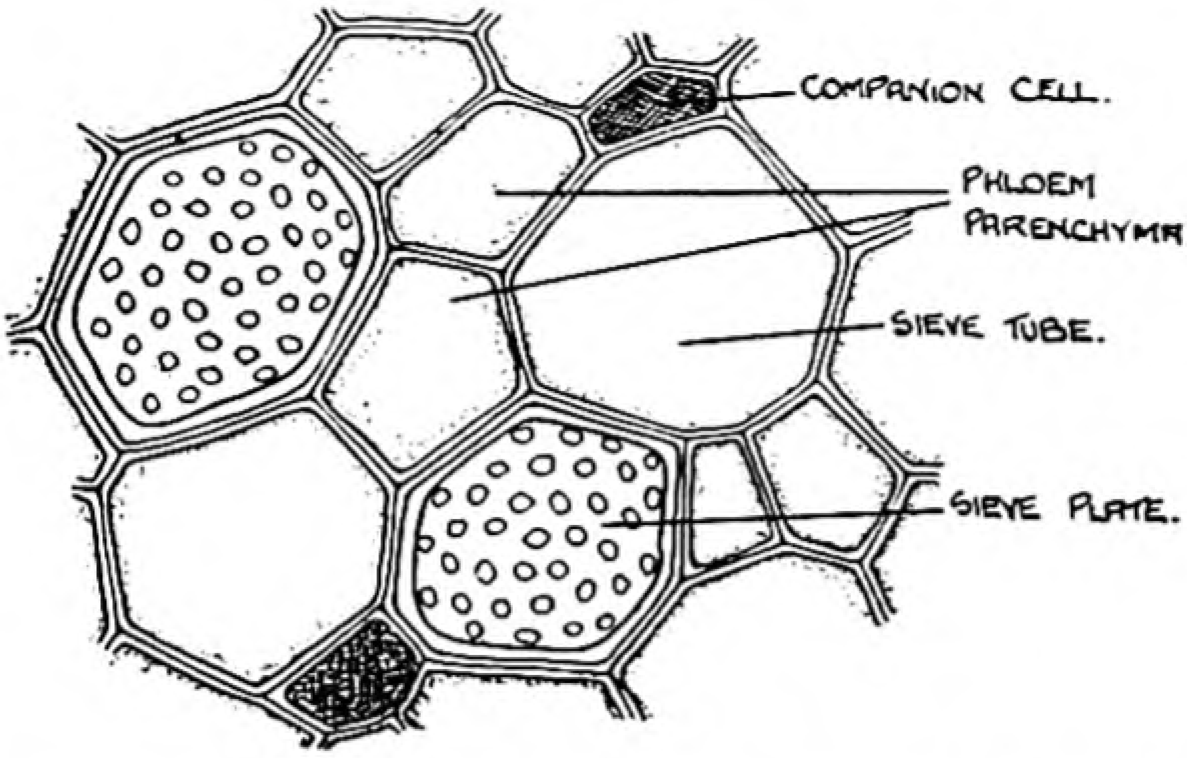

Fig. 25, A, *a*. PHLOEM, SIEVE-TUBES AND COMPANION CELLS, *Cucurbita*, TRANSVERSE SECTION.

Inside each segment there is a layer of cytoplasm, but the nucleus degenerates. The cytoplasm may contain a few leucoplasts and small starch grains. It is continuous through the pores of the sieve-plate. At certain times the sieve-plate is covered on each side by a layer of **callus**, consisting of a substance called *callose*. Callus is abundantly developed in the autumn, sometimes to such an extent that the pores of the sieve-plate are completely stopped up (e.g. in the vine). It is stained pink with alkaline solution of corallin. The contents of the sieve-tubes (enclosed by the protoplasm) are a watery cell-sap, alkaline in reaction, which is rich in albuminous substances, carbohydrates and inorganic salts.

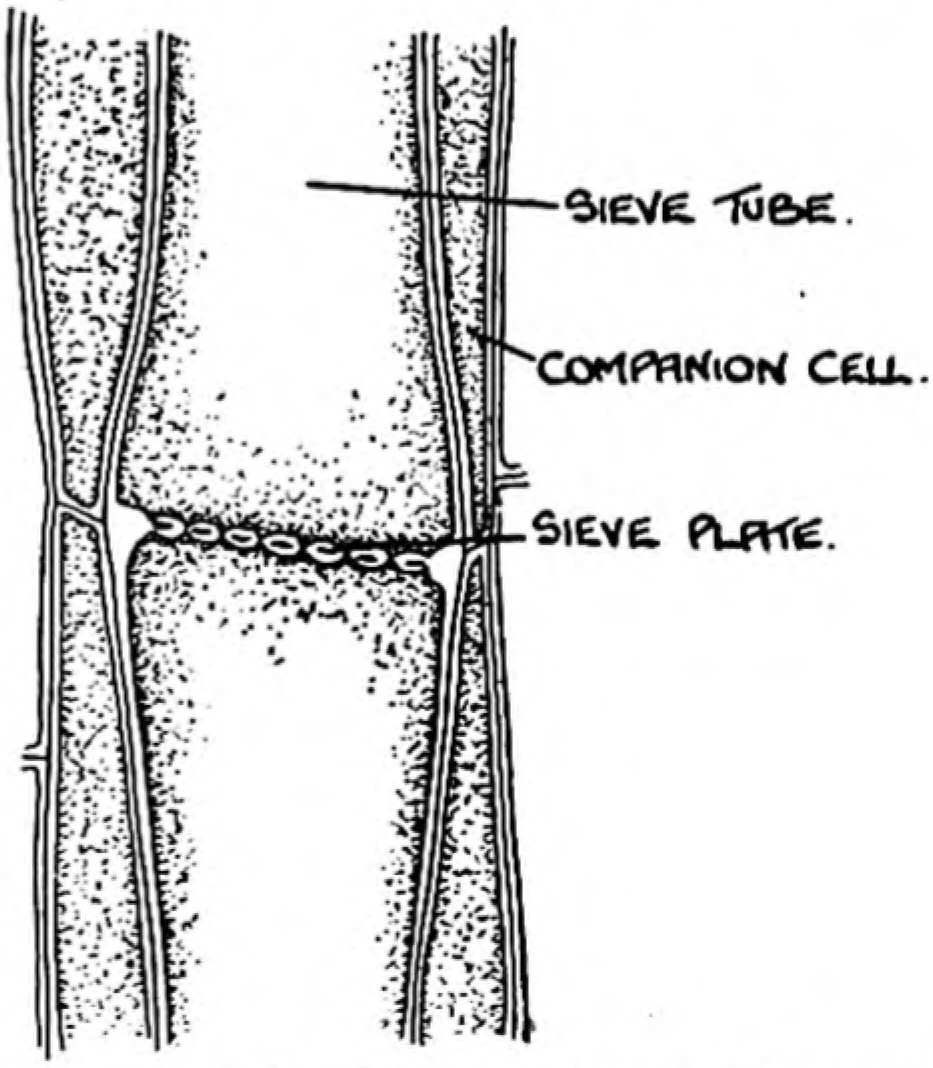

Fig. 25, A, *b*. LONGITUDINAL SECTION OF SIEVE-TUBE SHOWING SIMPLE SIEVE-PLATE.

Along with the sieve-tubes in Angiosperms are thin-walled elongated **companion cells,** so called because they are closely associated with the sieve-tubes, from which they are cut off during development.

Structures similar to the sieve-tubes of Angiosperms, consisting of elongated prismatic cells, are found in Gymnosperms and Vascular Cryptogams. Their sieve-plates are, however, most abundantly developed on the lateral walls and the perforations are small. They contain no starch. It should be noticed also that structures closely resembling sieve-tubes, are found in some of the larger Algae where there is a development of rudimentary conducting tissue.

Phloem serves for the transport of elaborated food-material to the various parts of the plant. A sieve-tube may function for one season only, and then be blocked by callus; but in some cases the callus is dissolved at the commencement of the next season and the function of the sieve-tube resumed.

27. (7) Laticiferous Tissue (Milk-Tubes)

This is a tissue found only in certain groups of plants. It consists of long, branching tubes, containing a characteristic substance, often milky in appearance, and called **latex.**

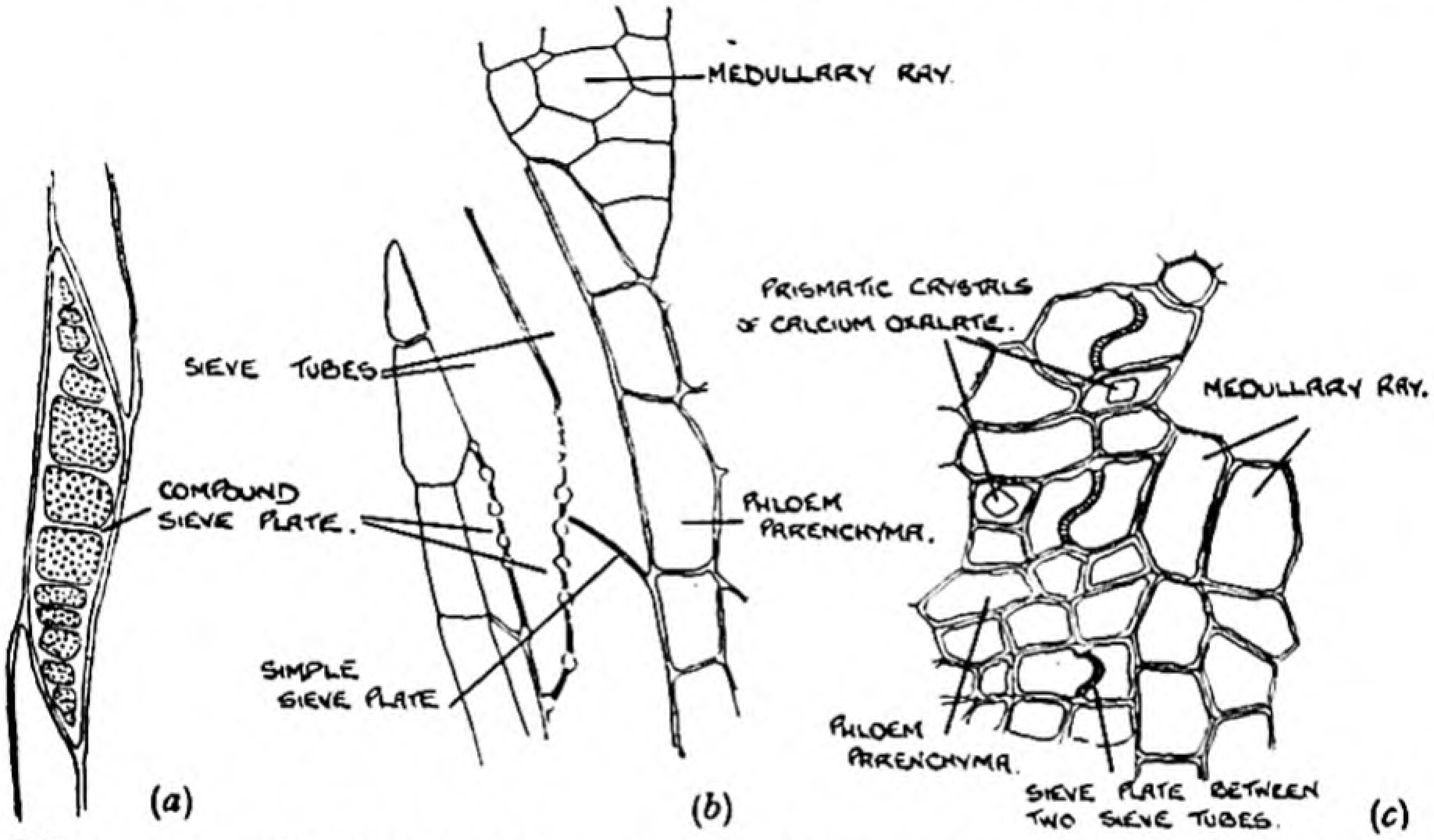
MEDULLARY RAY
SIEVE TUBES
COMPOUND SIEVE PLATE.
SIMPLE SIEVE PLATE
PHLOEM PARENCHYMA.
PRISMATIC CRYSTALS OF CALCIUM OXALATE.
MEDULLARY RAY.
PHLOEM PARENCHYMA.
SIEVE PLATE BETWEEN TWO SIEVE TUBES.
(a)
(b)
(c)

Fig. 25, B. PHLOEM OF *Rhamnus Purshiana*, SHOWING COMPOUND SIEVE-PLATES IN LONGITUDINAL (*a*) RADIAL AND (*b*) TANGENTIAL SECTIONS, AND (*c*) IN TRANSVERSE SECTION.

Two kinds of laticiferous tissue are recognised. The first kind consists of **vessels** formed by cell-fusion. Owing to the fact that the fusion takes place, not in definite longitudinal rows of cells, as is the case in wood-vessels, but in irregular series, the vessels not only are branched, but anastomose (*i.e.* the branches run into each other) to form a network (Fig. 26, A). The second kind consists of **cells.** In the embryo of a plant which possesses these, certain peculiar cells can be recognised. In development these cells elongate and branch, but transverse septa are not formed in them. There is, however, repeated mitotic division of the nucleus, so that these structures are really *coenocytes*, *i.e.* an aggregation of protoplasts enclosed in a common wall. Seeing that there is no cell-fusion, it is evident that the branches of these coenocytes do not anastomose (Fig. 26, B).

In both vessels and coenocytes the walls are somewhat thickened, but consist of cellulose; there is in both a lining layer of cytoplasm with nuclei. Laticiferous vessels are found in dandelion, poppy, and Hevea. Laticiferous coenocytes are found in Euphorbia.

The contained substance, the **latex**, presents different appearances in different plants. It is rarely quite watery (banana); usually it is more or less milky (*Euphorbia*), occasionally thick and coloured (in *Chelidonium* it has an orange colour). It consists of water containing various substances, either in solution or in suspension. These substances are usually of the nature of excreted products, so that the tubes are often to be regarded as reservoirs of excreted matter. Latex frequently contains substances of economic importance, used in medicine or industry. Opium is the dried latex of the opium poppy (*Papaver somniferum*) and contains alkaloids. Caoutchouc is derived from *Hevea* and *Ficus* species; guttapercha from *Palaquium* and *Mimusops*.

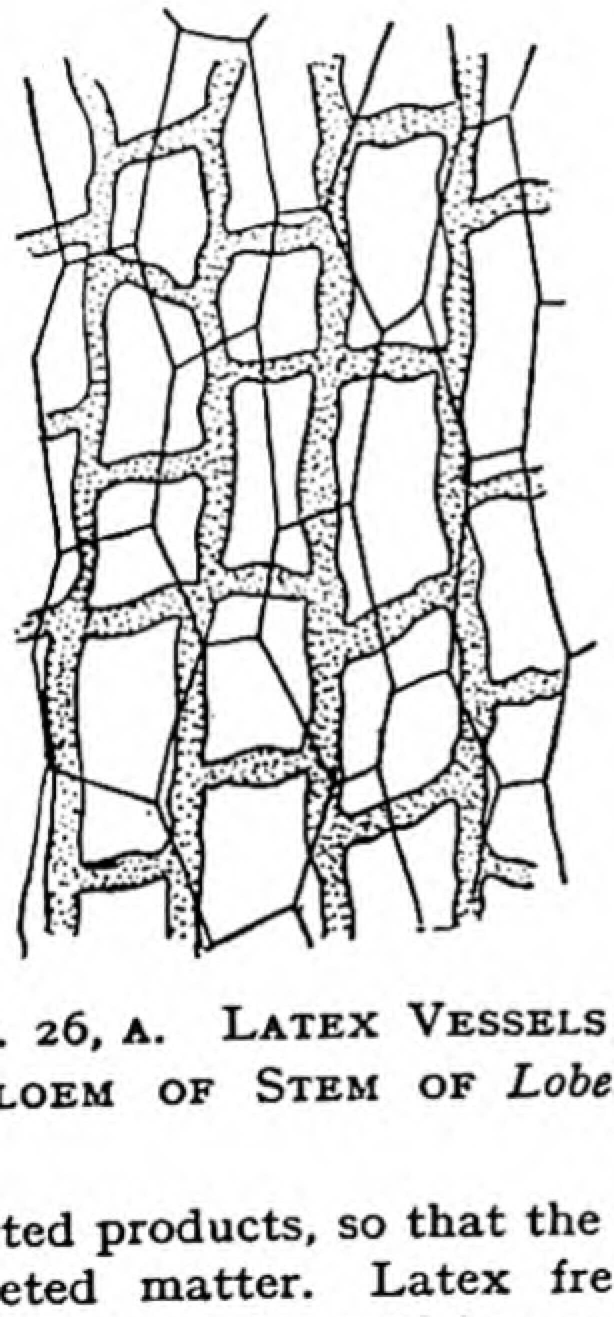

Fig. 26, A. LATEX VESSELS IN PHLOEM OF STEM OF *Lobelia*

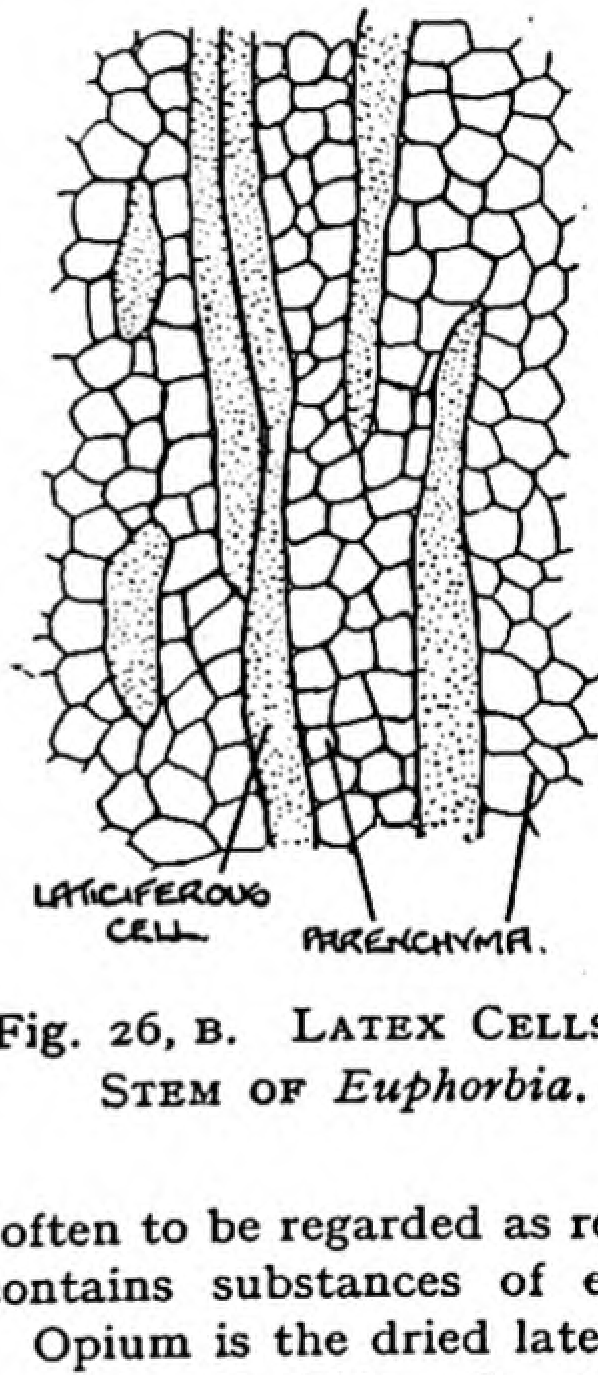

Fig. 26, B. LATEX CELLS IN STEM OF *Euphorbia*.

28. (8) Glandular Tissue

This tissue consists of structures of various kinds in which secreted or excreted substances are produced. Many of these have been spoken of as "secretion reservoirs." Although laticiferous tissue has been treated separately, it is not clearly marked off from this glandular tissue. The substances produced are of very varied character, such as gum, mucilage, resin, tannin, ethereal oil, water, etc.

Single cells (secretion cells or sacs) containing such substances are frequently found scattered through the tissues of plants. Such special cells in a tissue, which differ from the rest in structure or in contents or both, are examples of **idioblasts.**

Cells active in the secretion or excretion of water are found in some **hydathodes** on the margins or at the tips of leaves. The water which exudes to the surface often contains mineral salts in solution. When the water evaporates, these are left behind as an incrustation, frequently noticed in rock-plants. Further details of hydathode structure are given in Chap. VI, 21.

Closely allied to hydathodes are the multicellular glands forming the nectaries of flowers, the digestive glands of insectivorous plants, and the extra-floral nectaries which are found on some leaves (e.g. cherry). The sugary secretion of nectaries attracts insects to flowers and assists pollination. Extra-floral nectaries, at least in some instances, appear to attract certain types of insect, such as ants, which protect the plant against the depredations of other insects, whilst in insectivorous plants such as *Nepenthes* and *Sarracenia*, extra-floral nectaries act as a bait to insects.

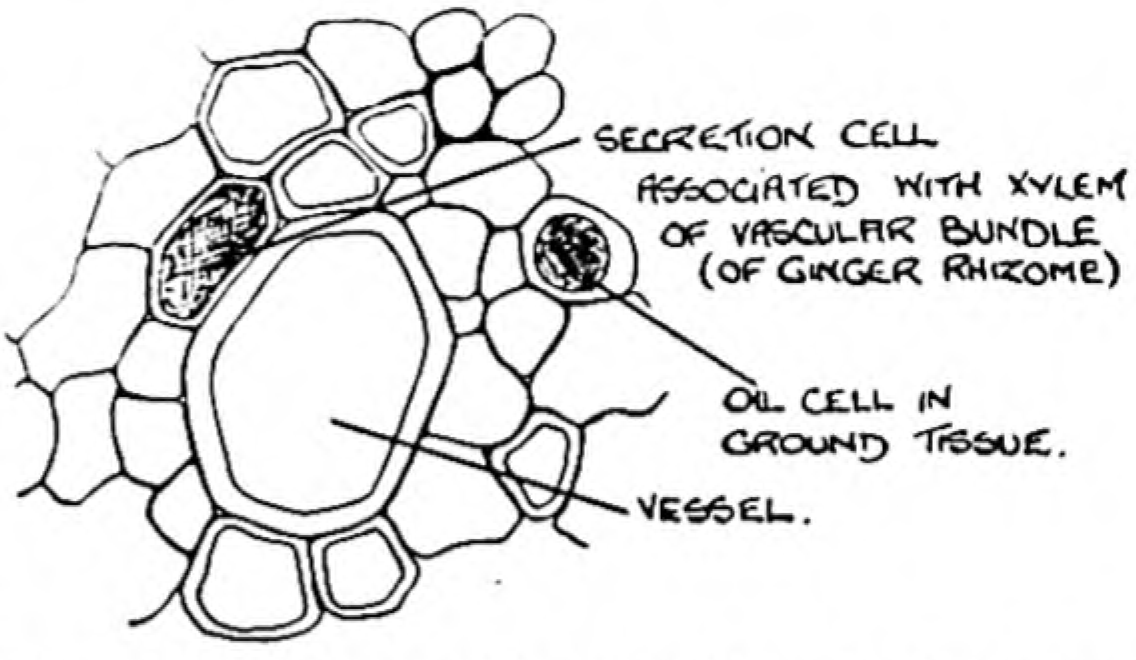
SECRETION CELL ASSOCIATED WITH XYLEM OF VASCULAR BUNDLE (OF GINGER RHIZOME)
OIL CELL IN GROUND TISSUE.
VESSEL.

Fig. 27. SECRETION CELLS OF *Zingiber* RHIZOME.
(T.S. Vascular Bundle.)

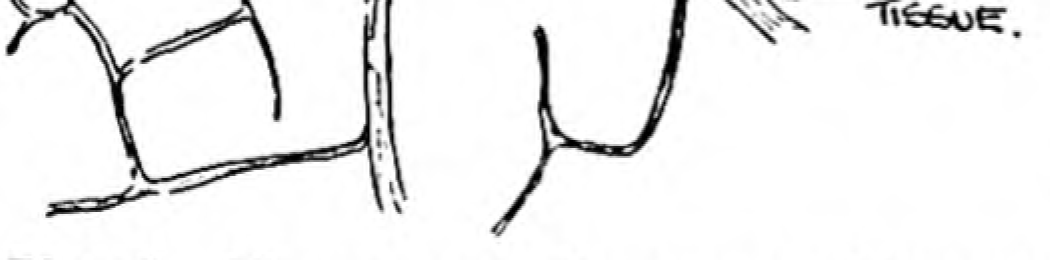

Fig. 28. HYDATHODE, GLANDULAR EPITHEM AS SEEN AT MARGIN OF LEAF OF *Lobelia*.
(Cleared Preparation.)

29. (9) Glandular Hairs

These vary considerably in form. They may be unicellular or multicellular, and in the latter case consist of a unicellular, uniseriate or multicellular pedicel and a uni- or multi-cellular head. In glandular scales the head is flattened or more or less concave. Secretions of mucilage and of ethereal oil or resin accumulate beneath the cuticle of the head cell or cells, causing its distension and final rupture. Examples of glandular hairs are seen on the leaves of members of the Solanaceae (*Atropa*, *Datura*, *Hyoscyamus*), Scrophulariaceae (*Digitalis*), Labiatae, and glandular scales on *Humulus*, *Mentha*, *Thymus*, etc.

Remarkable unicellular glandular hairs project into the intercellular spaces of the ground tissue of male-fern rhizome. The mucilage or resin produced in many winter buds (e.g. *Aesculus*) is formed by glandular hairs on the bud-scales.

Internal glands (secretory sacs or reservoirs) are classified according to their mode of origin. *Schizogenous* cavities are produced by the partial separation of the secretory cells to form an epithelium enclosing the cavity. *Lysigenous* cavities form as the result of the breaking down of the secretory cells when they have produced their secretion, which occupies the cavity thus formed. Glands which begin as schizogenous cavities, but later enlarge in a lysigenous manner, are referred to as *schizolysigenous* because of their composite origin. The oil sacs present in the rind (pericarp) of orange, lemon and grape-fruit are schizolysigenous. The resin-ducts of *Pinus* and the oil-sacs (vittae) of fruits of Umbelliferae, e.g. fennel, coriander and cumin are schizogenous. The leaves of *Citrus* species possess lysigenous oil-glands.

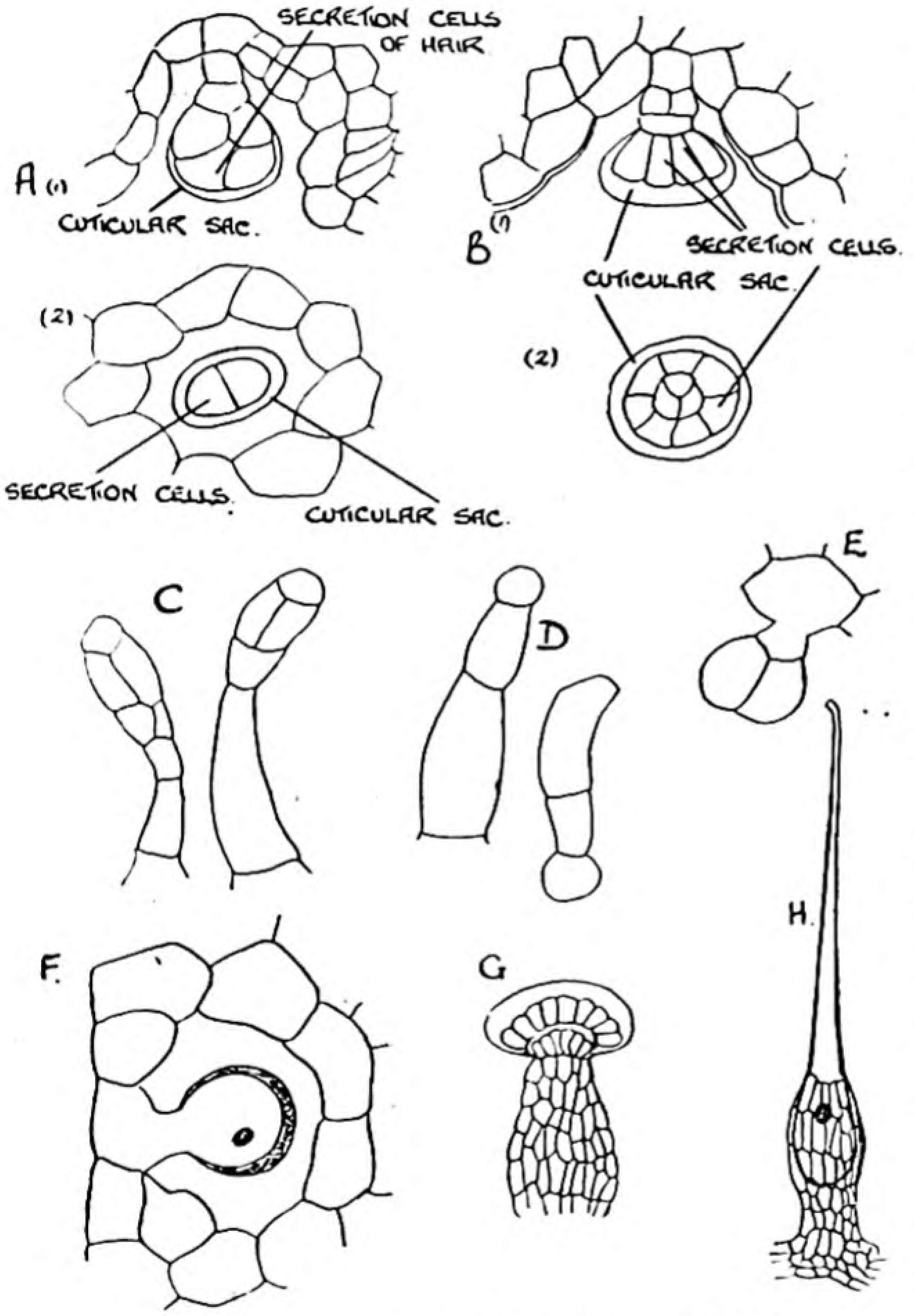

Fig. 29. TYPES OF GLANDULAR HAIRS.

A, *Artemisia* and B, *Thymus* in section and surface view; C, *Hyoscyamus*; D, *Atropa*; E, *Digitalis*; F, *Dryopteris Filix-mas* Rhizome; G, *Cannabis*; H, *Urtica dioica*.

Digestive glands are present in insectivorous plants. They secrete protein-digesting enzymes, and these enzymes act upon small insects captured by the leaves. *Drosera*, the sun-dew, has secretory glandular hairs, which not only hold the insect by their sticky secretion, but are sensitive to touch and imprison the insect by bending over it. (See pages 201, 224.)

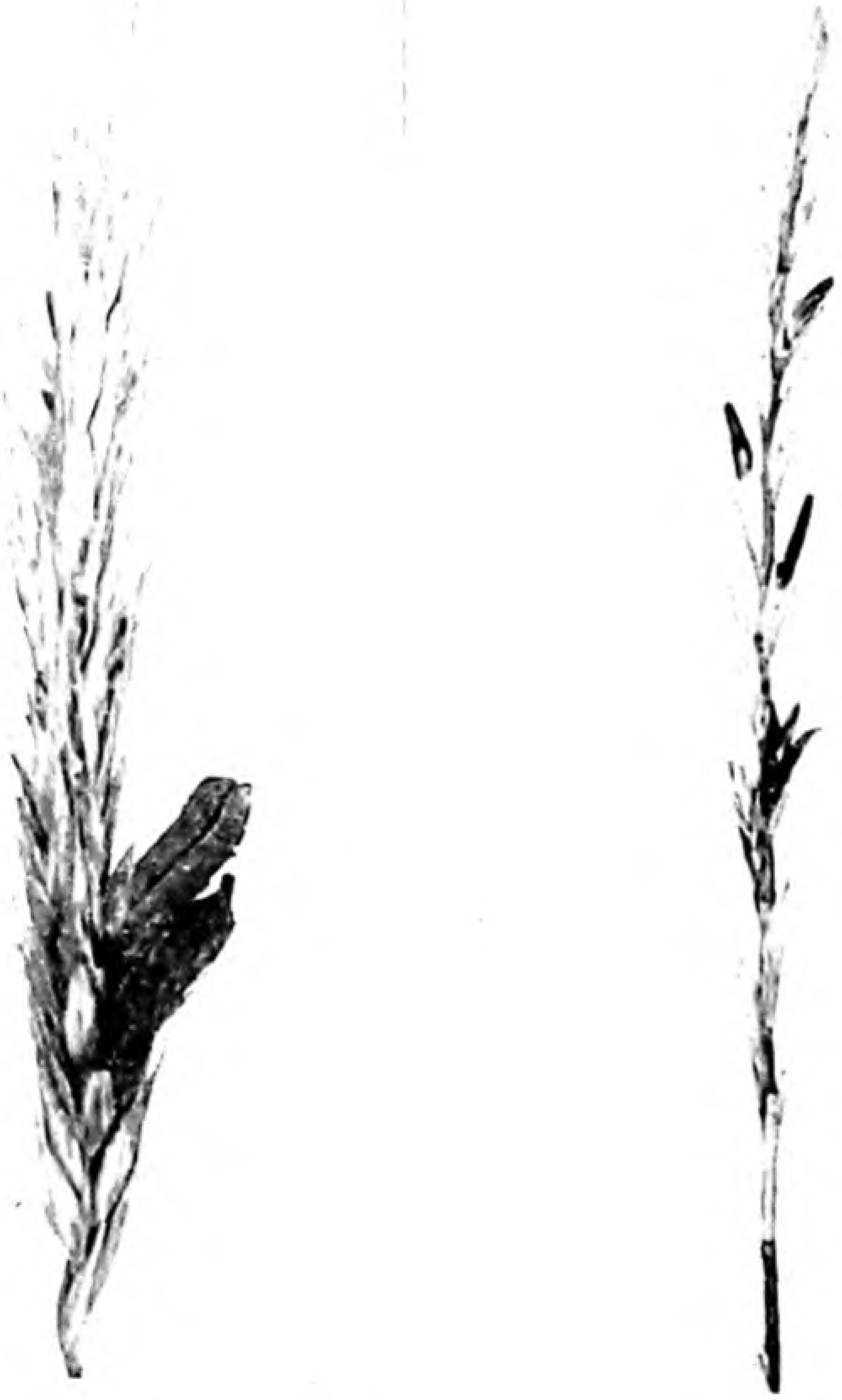

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Photo: Dr. J. H. Western.

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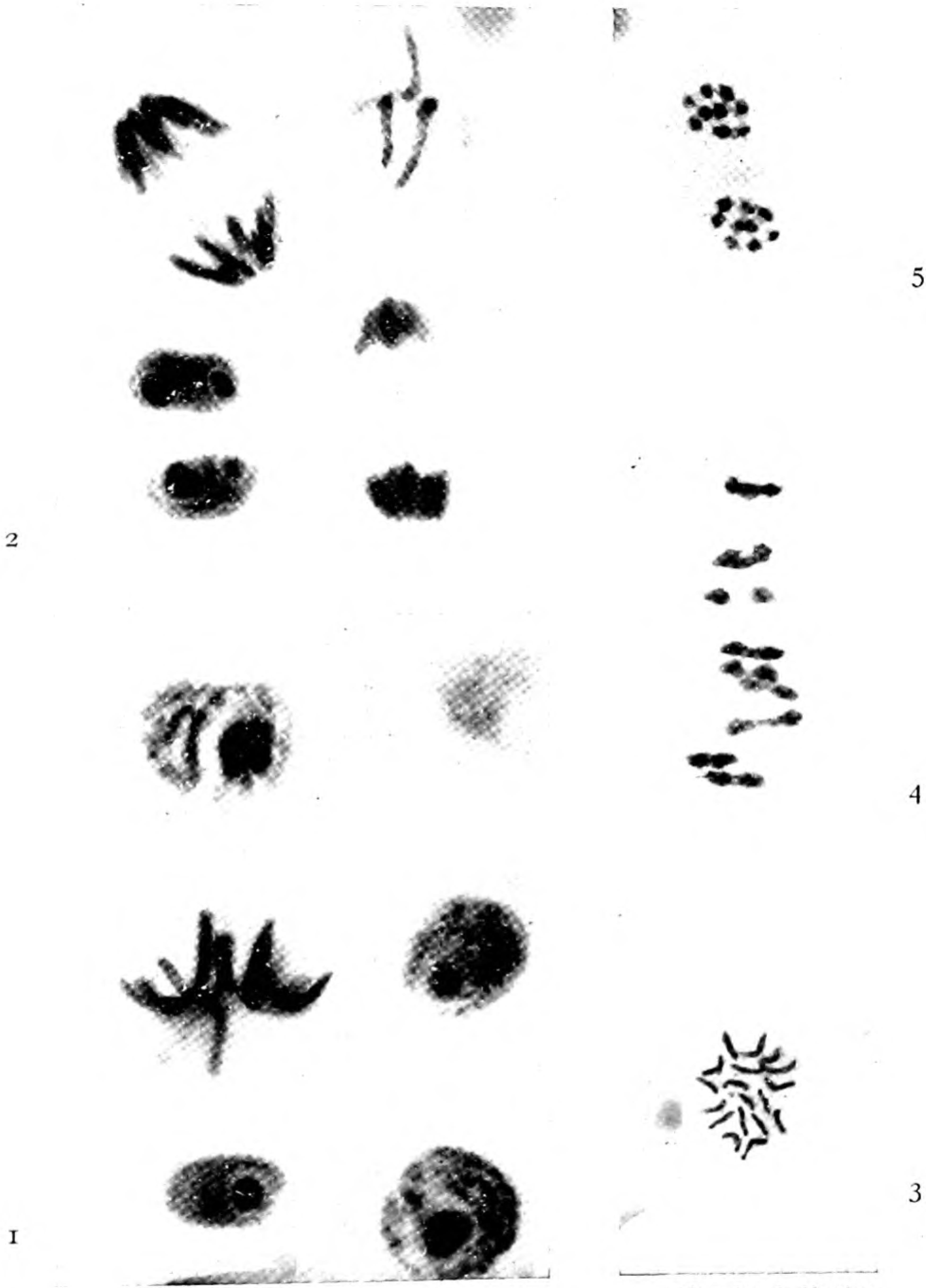
PLATE III

SCLEROTIA OF ERGOT.

1. *Secale cereale.* 2. *Lolium perenne.*



After Dr. I. Manton.

PLATE IV

MITOSIS AND MEIOSIS.

1 and 2. Cells in Mitosis from root of diploid *Allium ursinum*, cut longitudinally, stained iron-alum-haematoxylin, × 1000. 1 shows Resting, Prophase and Metaphase; 2, Anaphase, early and late Telophase, and a cut Metaphase. 3, Chromosome count from root-tip of diploid *Biscutella laevigata*, stained gentian violet, × 2000. $2n=18$. 4 and 5. Pollen-mother-cells from same species. 4 shows first meiotic division, chromosome pairing, × 1500; 5, Metaphase of second meiotic division, two nuclei each with 9 chromosomes, $n = 9$, × 2000.

C. TISSUE-SYSTEMS

The different forms of permanent tissue which we have just described are aggregated in various ways to form *tissue-systems.* We have noticed (§ 20) that the differentiation of these tissue-systems takes place gradually, and that they reach maturity some distance behind the growing point. This will be understood more easily by reference to Fig. 32, which illustrates the development and differentiation of the vascular tissue system in a *Brassica* seedling. Immediately behind the dome-shaped stem apex there occur exogenous outgrowths which, in the course of their development, gradually take shape as leaves. At an early stage in the development of each leaf, first one (middle), then two more (lateral), then two more again (lateral to the former), "desmogen" strands appear. These strands can be followed down into the stem, where they form a ring with similar strands from other leaves. At first the desmogen strands are undifferentiated meristematic tissue common to leaf and stem. Very soon, however, spirally thickened protoxylem elements become apparent. They are recognisable in the very

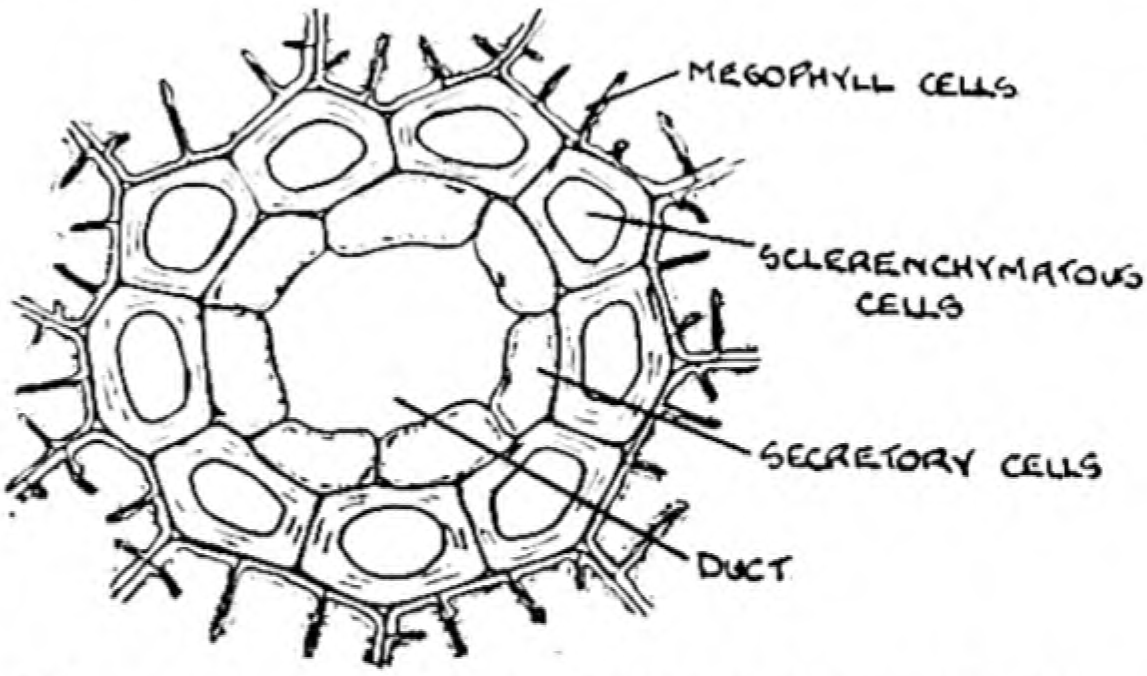


Fig. 30, A. INTERNAL SCHIZOGENOUS GLAND.
(Resin duct of *Pinus.*)

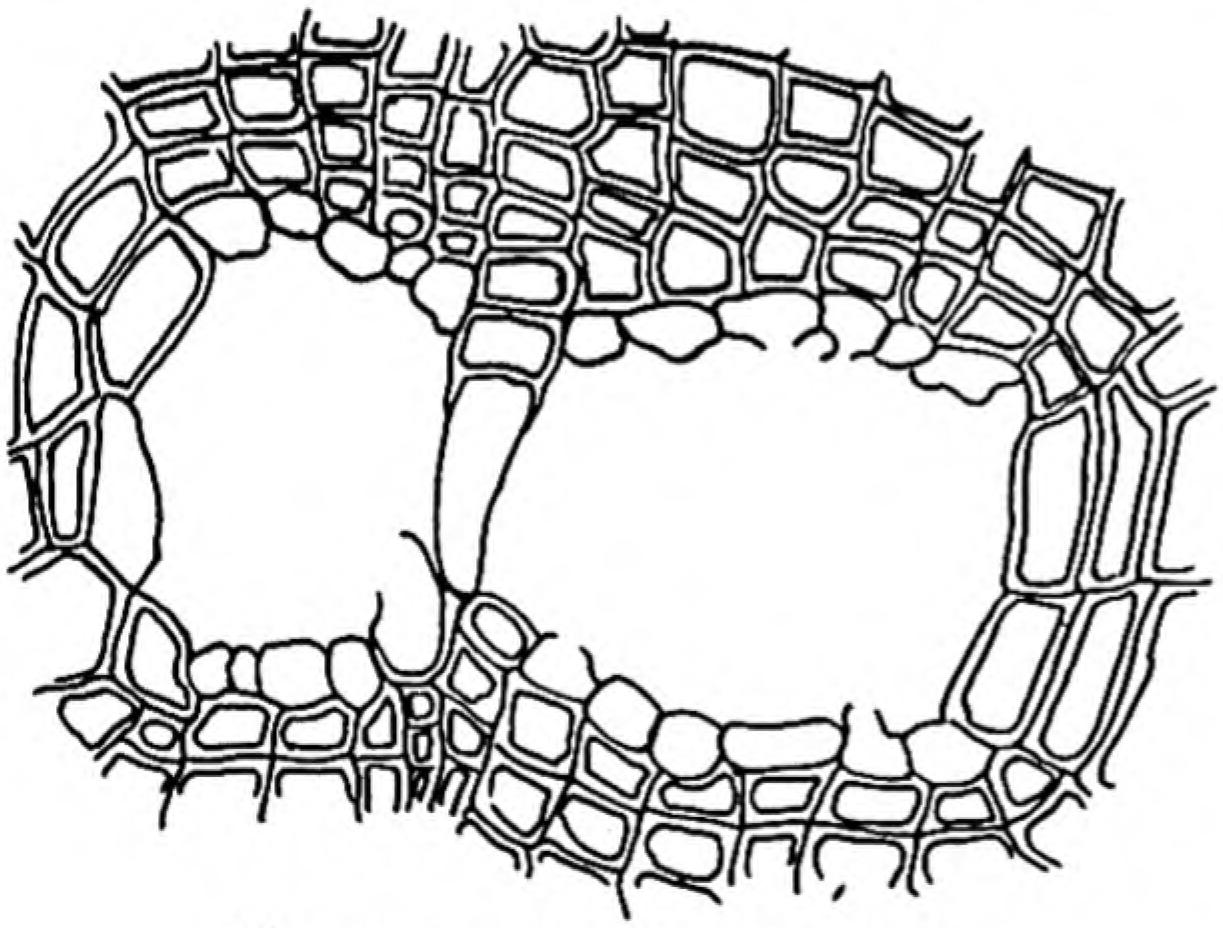


Fig. 30, B. LYSIGENOUS GLANDS.
(Secondary Xylem of *Copaifera.*)

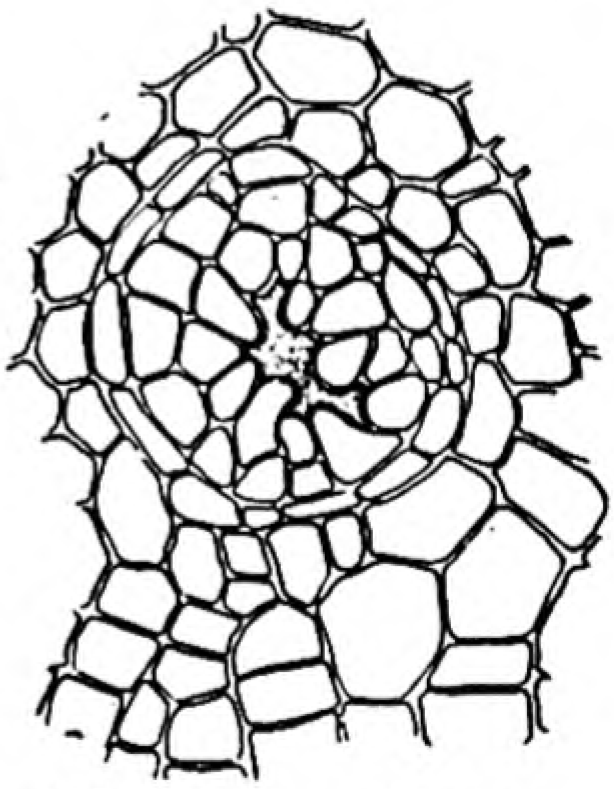


Fig. 30, C. YOUNG SCHIZOLYSIGENOUS GLAND.

young leaves which grow more rapidly than the stem apex and overtop it, and they are found to be continuous with similar elements which differentiate on the inside of the desmogen strands in the stem at points corresponding to the insertion of the leaf-trace bundles. Recognisable phloem elements differentiate later, on the outside of the desmogen ring. Also, at about the same level, recognisable sclerenchymatous fibres appear. These are immediately outside the phloem and form the pericycle which bounds the central cylinder (stele). Hence, in *Brassica*, it is only at this stage that the distinction between cortex and stele can be recognised. Behind the apex it is only possible to distinguish dermatogen from the central mass of undifferentiated cells.

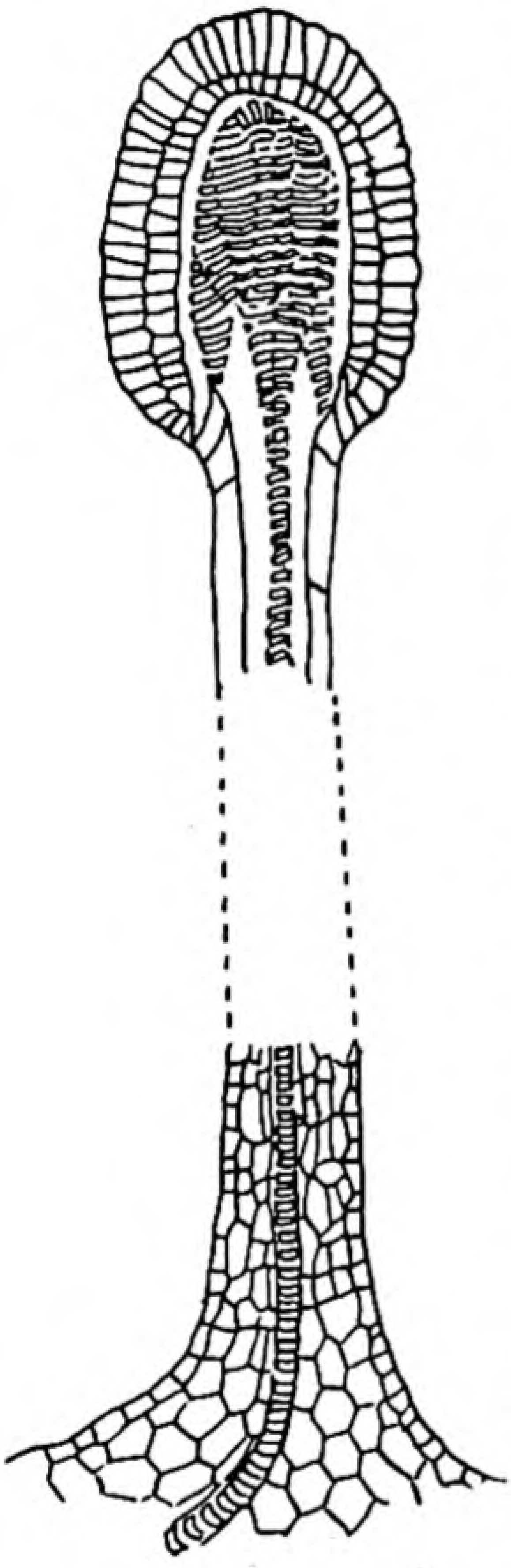


Fig. 31. DIGESTIVE GLAND OF *Drosera*.

The features which the tissue systems present in their mature state are described below.

30. The Epidermis

The epidermis consists of a single layer of cells which at first covers stem, root and leaf. As we have seen, it is the product of the dermatogen, which divides by walls at right-angles to the surface (anticlinal walls), with some exceptions; the resulting cells become variously shaped, as seen in surface view. Its main function in the shoot is to *protect* the plant from injury and to conserve the water supplied by the roots; in the root, to obtain water from the soil. The cells are living and vacuolated. Chloroplasts may be present in certain specialised epidermal cells called guard-cells (see stomata), or in all the epidermal cells of plants growing in the shade, or in water. In plants subject to periods of drought the epidermal cells may contain mucilage and store water, and in such plants the epidermis of the leaves may consist of two or more layers of cells. The so-called velamen of the aerial roots of orchids may be regarded as a many-layered epidermis.

The *epidermal cells* of a one-layered epidermis are always more or less flattened or tabular. Their outline, when seen in surface view, is various. As a general rule, however, they are considerably elongated in the direction of the length of the organ, e.g. stems and many monocotyledonous leaves (Fig. 33, A); while in organs about as broad as long, they are not elongated, but have an extremely wavy outline, e.g. most dicotyledonous leaves (Fig. 33, B).

As already indicated, the outer walls are cuticularised, and this prevents evaporation from the tissues. Frequently also the cuticle is covered with a thin layer of wax ("bloom"), which prevents the surface being wetted and retards the giving off of water vapour.

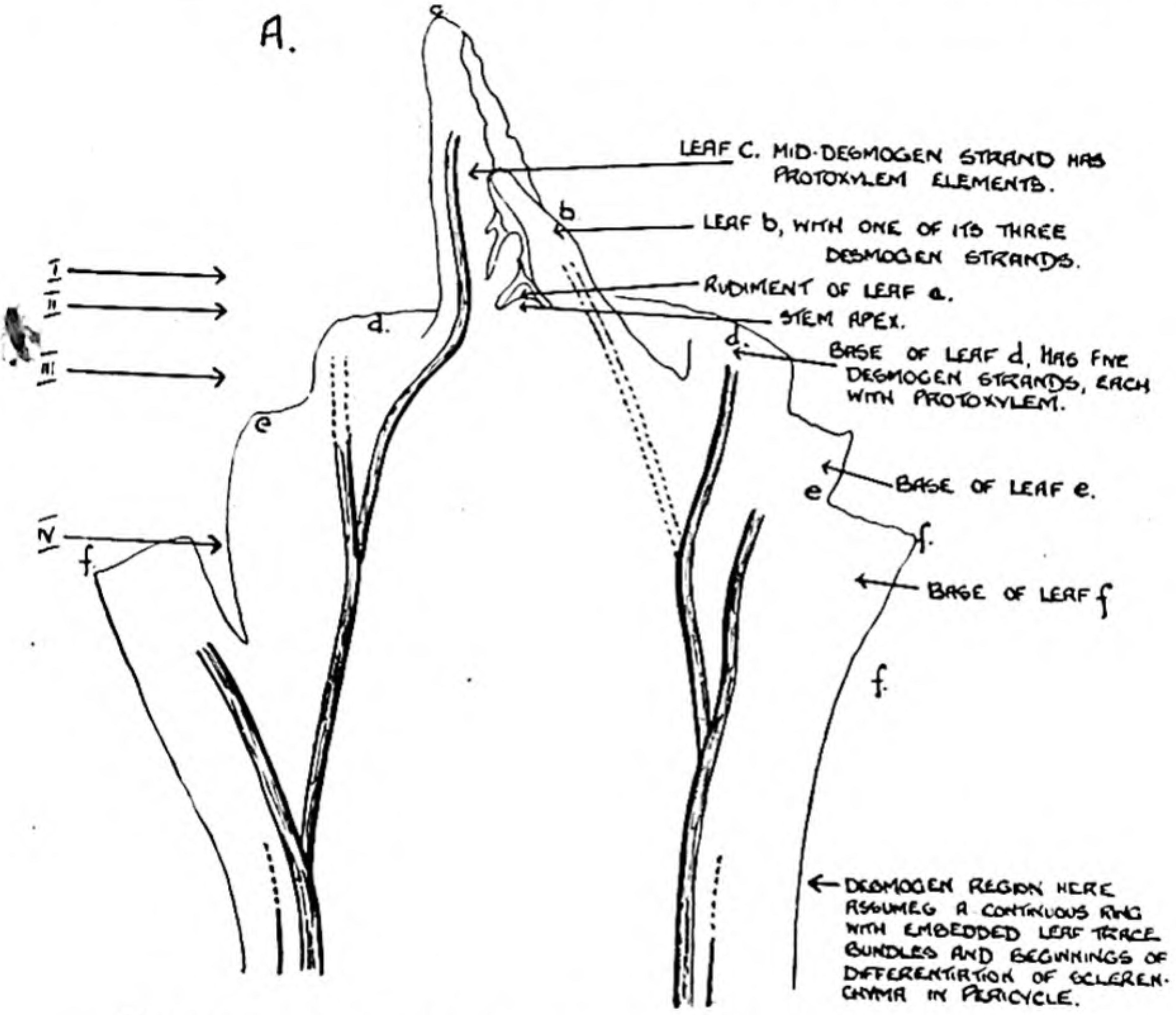

A.
a
I
II
III
IV
LEAF C. MID-DESMOGEN STRAND HAS PROTOXYLEM ELEMENTS.
b
LEAF b, WITH ONE OF ITS THREE DESMOGEN STRANDS.
RUDIMENT OF LEAF a.
STEM APEX.
d.
d.
BASE OF LEAF d, HAS FIVE DESMOGEN STRANDS, EACH WITH PROTOXYLEM.
e
e
BASE OF LEAF e.
f.
f.
BASE OF LEAF f
f.
DESMOGEN REGION HERE ASSUMES A CONTINUOUS RING WITH EMBEDDED LEAF TRACE BUNDLES AND BEGINNINGS OF DIFFERENTIATION OF SCLEREN-CHYMA IN PERICYCLE.

Fig. 32, A. Apical Differentiation in *Brassica* Seedling.

The cuticle and waxy bloom are most strongly developed in plants which live in bright sunlight (sun-plants), or in dry places. In shade- and moisture-loving plants the cuticle is poorly developed, and it is absent from roots and the submerged parts of aquatic plants.

31. Guard-cells and Stomata

The stomatal or guard-cells are so called because they surround or guard the openings, known as stomata (Fig. 34, A and B), numerously developed in the epidermis of aerial parts. These stomata

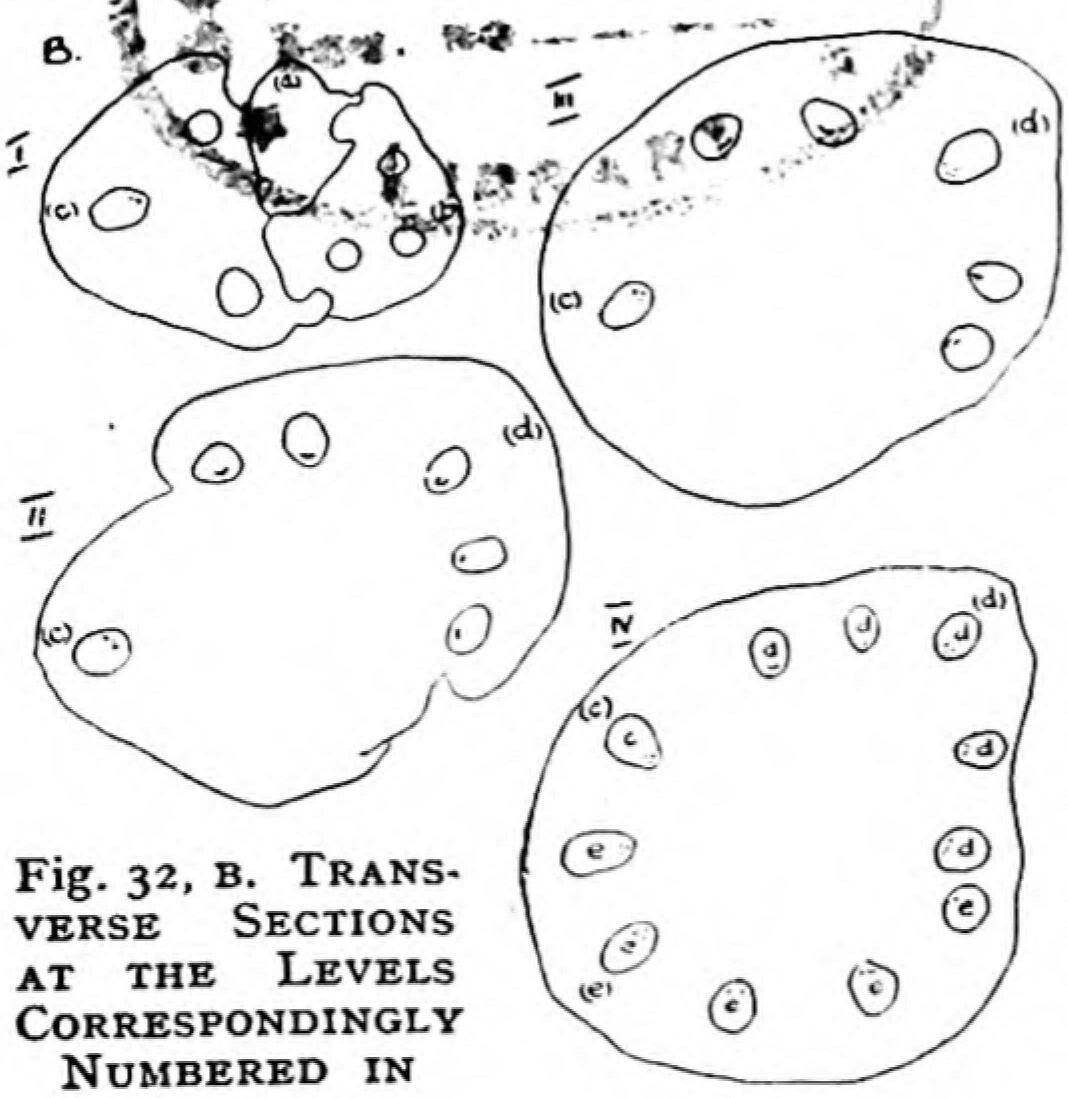


Fig. 32, B. TRANSVERSE SECTIONS AT THE LEVELS CORRESPONDINGLY NUMBERED IN FIG. 32, A.

communicate with the system of intercellular spaces in the underlying tissues, and serve, as we shall see later, as a means of gaseous interchange between the plant and the atmosphere.

Usually each stoma is surrounded by two guard-cells—one on each side. The guard-cells are crescentic in form. They always contain cytoplasm, nucleus, and numerous chloroplasts. Their walls are thickened; the thinnest in each guard-cell is that which is farthest from the pore. The guard-cells alter their form, and thus increase or diminish the size of the opening. In this way they may regulate the amount of water-vapour passing out of the plant in the process of transpiration. Sometimes other small cells (*subsidiary cells* of the stoma) lie outside the guard-cells.

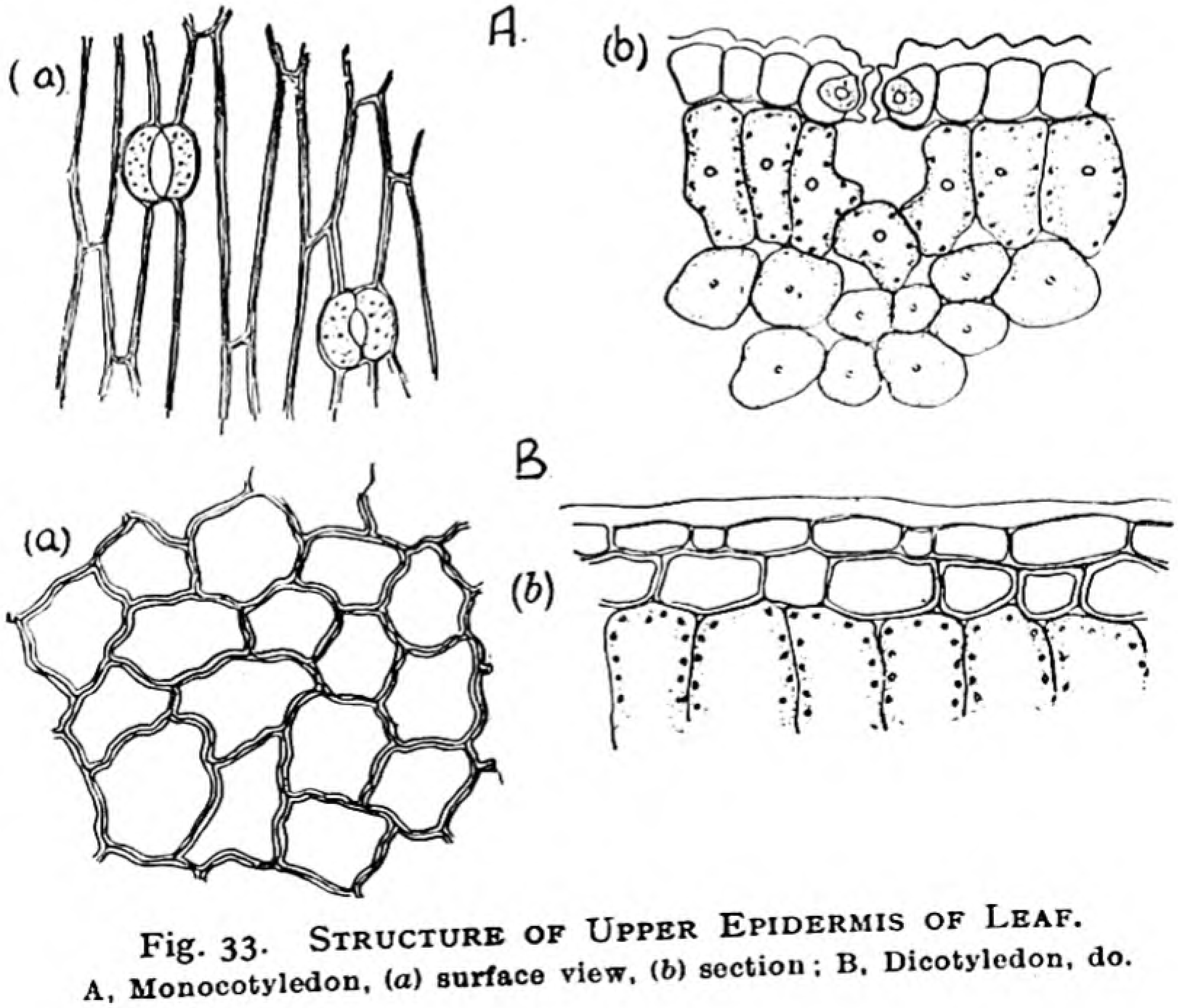


Fig. 33. STRUCTURE OF UPPER EPIDERMIS OF LEAF.
A, Monocotyledon, (*a*) surface view, (*b*) section; B, Dicotyledon, do.

In the development of a stoma, a small cell, the mother-cell of the stoma, is cut off from a young epidermal cell. A cell-wall then divides the mother-cell into the two guard-cells. The pore is formed by the splitting of the common wall between the guard-cells. Subsidiary cells, when present, are formed by the division of the surrounding epidermal cells.

32. Position of Stomata

Stomata may be developed on all *aerial* leaf and stem structures —even on the ovary and anthers of the flower. They occur on the spore-capsules of many Bryophyta, but with this exception they are confined to the Vascular Cryptogams and Seed Plants. They are not developed on roots or submerged parts. On green foliage leaves, where they are most numerously developed, their number and position depend largely on the position and direction of the leaf, and on the conditions with regard to transpiration. In bifacial leaves (p. 140) they are usually most abundant on the lower surface, sometimes confined to it. On floating leaves, e.g. leaves of the water-lily, they are found on the upper surface. In some bifacial leaves, but more especially on vertical leaves (isobilateral leaves, e.g. the iris), they are about equally distributed on both surfaces.

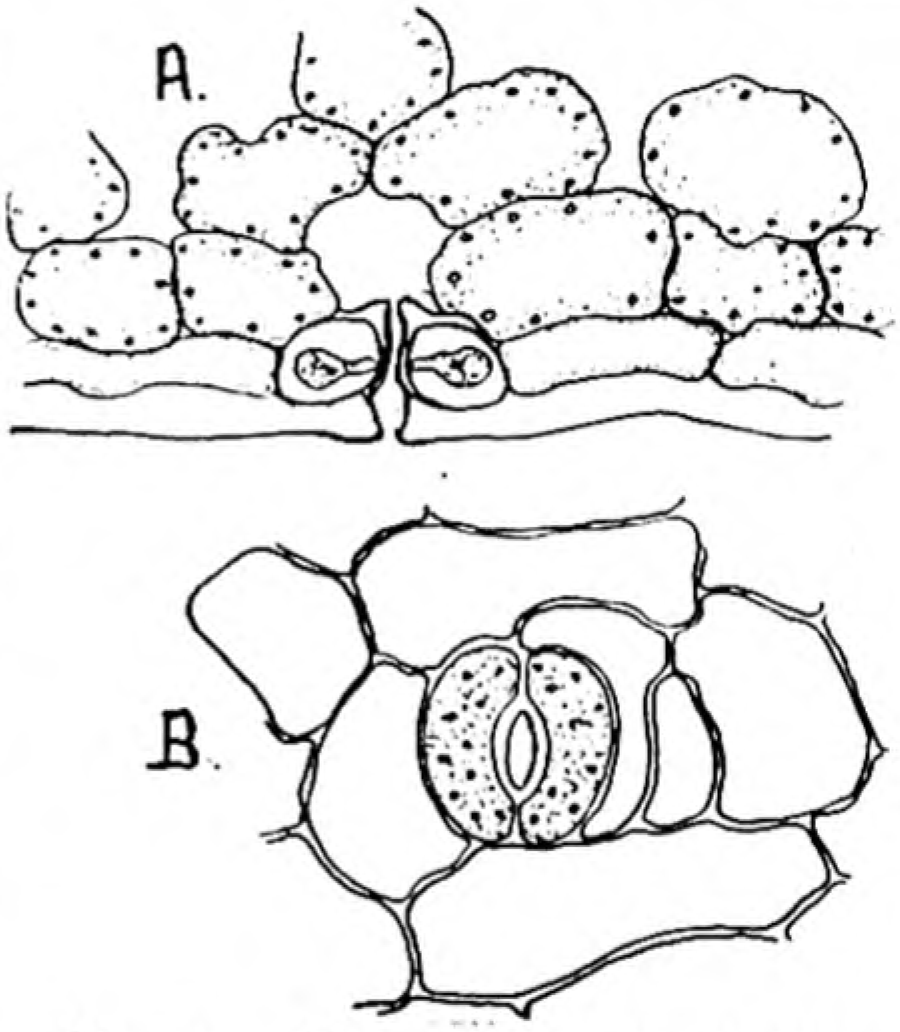


Fig. 34. STRUCTURE OF STOMA, LEAF OF *Prunus Laurocerasus*.
A, Section; B, Surface View.

33. Hairs or Trichomes

Hairs or *trichomes* arise from one (unicellular) or more (multi- or pluri-cellular) epidermal cells, and are of varied character. The simplest are the *papillae*, frequently met with on the petals of flowers, giving the velvety appearance of these organs. Papillae are the somewhat cone-shaped outward extensions of the exposed walls of epidermal cells. A short distance behind the growing-points of roots we find much longer extensions of the outer wall of the epidermis, the wall remaining thin and the cell living and vacuolated, with a nucleus embedded in the thin peripheral cytoplasm near the tip of the hair. These are the root-hairs on account of which the name *piliferous layer* is given to the epidermis of the root. They enormously increase its absorbing surface.

Other much elongated, unicellular hairs, but with thickened cellulose walls covered with a thin cuticle, are those of the epidermis of the seed of the cotton plant (*Gossypium* species) which provide the cotton of commerce. These hairs, when fully mature, are dead and filled with air, hence their white appearance. They are also twisted and more or less flattened. Short, thick-walled and sharply pointed unicellular hairs, bent or curved all in one direction, make the surface of the organ which bears them rough to the touch (*scabrous*), whilst longer, straight, stiff hairs are usually termed ***bristles***, and may have their walls impregnated with silica or calcium carbonate. When the surface of a hair, as seen under a microscope, is raised in numerous slight, rounded projections, it is said to be warty.

When a multicellular hair consists of a row of two or more cells, it is described as uniseriate. Multicellular hairs may have a massive base involving a number of epidermal cells, but tapering to a single cell at the tip; they may be stellate, consisting of several unicellular hairs arising from a common basal cell; or candelabra hairs, when the stellate hairs are arranged in two or more tiers; scale-hairs, consisting of a plate of cells radiating from a common centre of attachment; ramentae, consisting of a plate of cells attached laterally; capitate hairs, with a definite pedicel and a rounded or flattened head. Often such hairs are glandular [see § 29 (9)]. Hairs other than glandular are usually classified as covering or protective; hairy surfaces are variously described according to the character of the hairiness, e.g. pubescent, pilose, ciliate, etc. Such hairs may protect leaves and stems against excessive loss of water by transpiration. They sometimes form a felt-like layer over the surfaces of young leaves, especially in winter-buds.

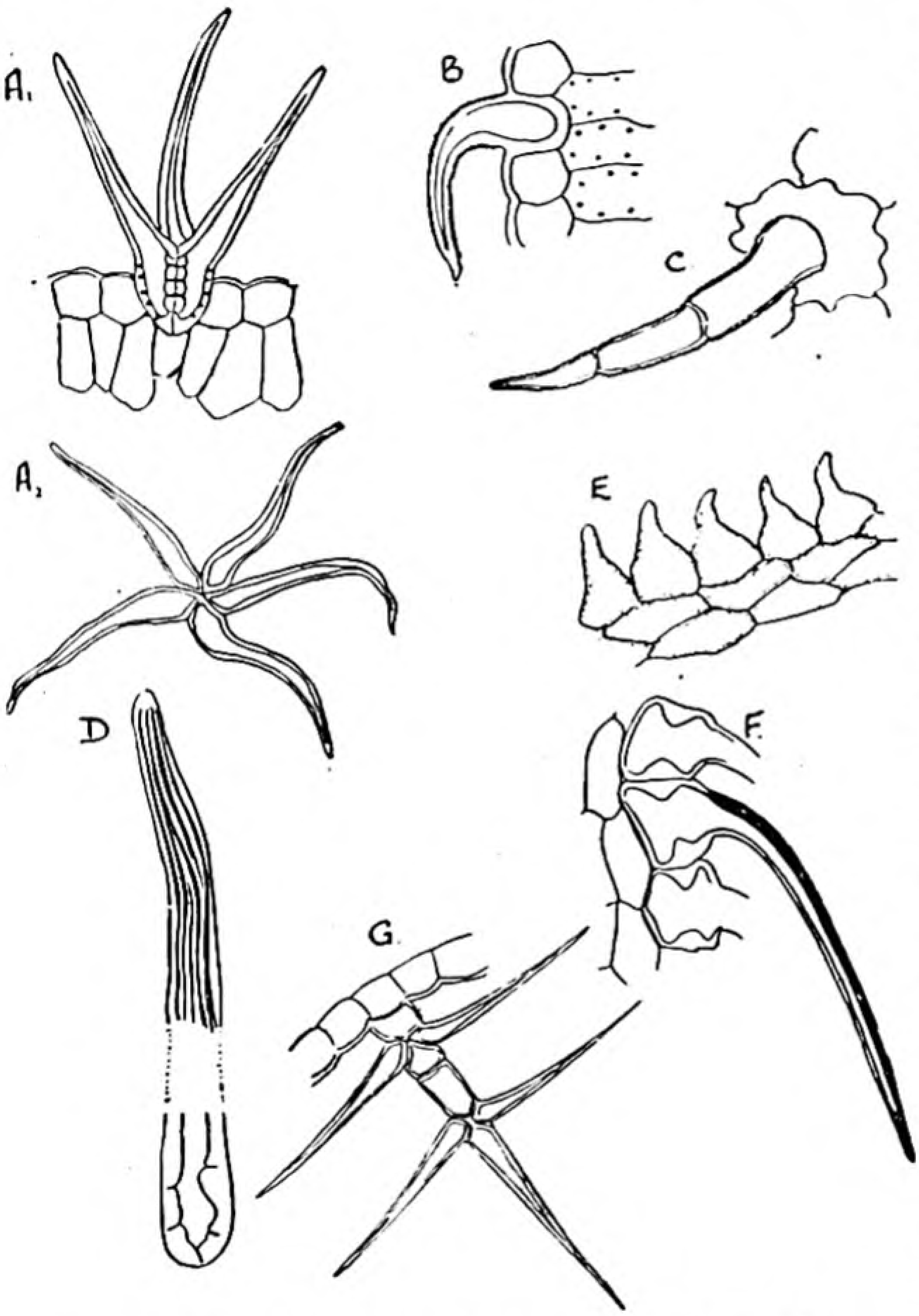


Fig. 35. VARIOUS KINDS OF TRICHOMES.

A1 & A2, Leaf of *Hamamelis*; B, Leaf of *Cassia*; C, Leaf of *Datura*; D, Testa of *Strychnos Nux Vomica*; E, Petal of *Arnica*; F, Testa of *Strophanthus*; G, Leaf of *Verbascum*.

Protection in another sense is afforded by such hairs as those of the stinging nettle (*Urtica dioica*, Fig. 29, H), Nilgiri nettle (*Girardinia heterophylla*), and some species of *Laportea*. In *Urtica* these consist of an elongated, tapering hair whose broader, rounded base is embedded in a columnar mass of epidermal cells. When a nettle is touched, the brittle siliceous point of a hair breaks and a puncture is made in the skin. The contents of the hair, which were evidently under pressure, are forced into the skin by the release of the pressure, assisted by a contraction of the base of the hair. The hair contains formic acid, and the injection produces local inflammation and swelling.

Emergences.—Stronger outgrowths often found on the surface of the plant which differ from trichomes in containing a core of cortex (occasionally also vascular tissue) are called emergences. Examples are the **prickles** of the rose (Fig. 36) and the *membranous* outgrowths, called **ligules**, of e.g. the leaves of grasses (Fig. 99, D), and the petals of *Dianthus*.

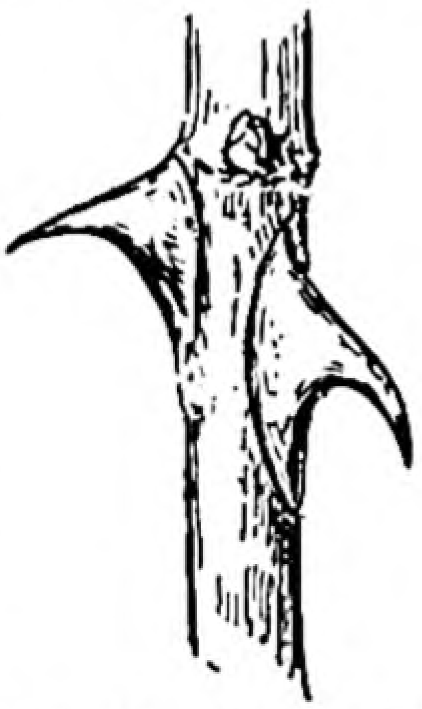


Fig. 36. PRICKLES OF *Rosa*.

34. Water-Pores or Water-Stomata

Other openings, closely resembling stomata in appearance, but differing from them in important respects, are frequently found on leaves, e.g. in *Fuchsia* and *Tropaeolum*. They are called *water-pores* or *water-stomata*, because, instead of giving out water-vapour, they excrete drops of water. They are often found associated with active secretory tissue in hydathodes. (See Chap. VI, § 21; also this Chap., § 28.)

35. The Vascular System

This provides for the rapid movement of water and food-materials in the plant. It is *a continuous system in stem, leaf, and root.* In herbaceous plants it usually consists of a varying number of strands or bundles—**vascular bundles**—running longitudinally through stem and root, and passing out into the leaves at all levels. These bundles consist essentially of phloem and xylem. In stems and roots of woody plants, owing to further meristematic activity, this arrangement in bundles is modified, and stout cylinders of phloem and xylem are produced. At present, however, we shall confine ourselves to the general characters of a vascular bundle.

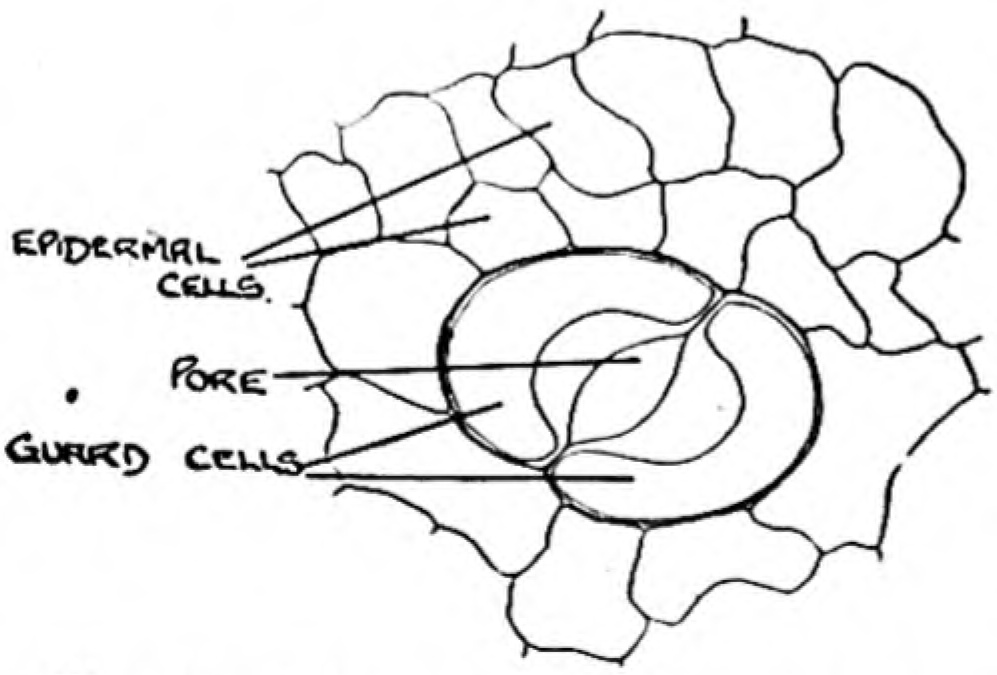


Fig. 37. WATER STOMA, EPIDERMIS OF *Lobelia*.

36. The Vascular Bundle

Vascular bundles (see Figs. 64, 65, 82, etc.) may consist of xylem only, or of phloem only, as in roots; or, as in stems and leaves, of both xylem and phloem. The xylem essentially contains tracheal tissue (vessels, tracheides) (§ 26). Associated with this, however, there are parenchymatous cells, either thin-walled or thickened and lignified, called **xylem-parenchyma,** and frequently also sclerenchymatous fibres, called **xylem-fibres.** The phloem essentially contains sieve-tubes (§ 27), but associated with it, in Angiosperms, are companion cells (Fig. 25), and usually, also, other cells known as **phloem-parenchyma.**

To the outer side of the phloem in many bundles there is a group of sclerenchymatous fibres. In leaves the bundles spread out and form the veins; the veins end in various ways.

37. Ground-Tissue System

This system consists of many different kinds of tissue, and has many functions to discharge. The most abundant tissue is thin-walled parenchyma; but associated with this are other tissues in varying amount—sclerenchyma, collenchyma, laticiferous tissue, and glandular tissue. Very frequently this system is marked out into distinct regions, such as the *pith,* the *cortex,* the *medullary rays,* the *hypodermis,* the *endodermis* or bundle-sheath, the *pericycle.* All these will be described in due course.

PART II—THE ANGIOSPERM

CHAPTER III

SEED AND EMBRYO

1. Before proceeding to a detailed consideration of the form and structure of the parts of the adult plant, it is proposed to examine their earliest forms as found in the embryo. This may be done by studying the structure and germination of a few seeds. The study is essentially a practical one and should be carried out by the student. The following descriptions and figures, therefore, are merely intended to help and direct this work.

2. The Sunflower Seed

The so-called sunflower seeds of commerce (Fig. 38) are really the fruits of *Helianthus annuus*, each containing one true seed. They were attached to the parent plant by the pointed end. Before examination they should be soaked in water for about 24 hours. The wall of the fruit is called the **pericarp.** It is dry and thick, and can be removed by means of a penknife or scalpel. The seed which lies inside is invested by a thin yellowish or brownish membrane, constituting the seed-coat and called the **testa.** The removal of this discloses a rather fleshy embryo plant, pointed at one end. The pointed end is called the **radicle** and is the young root. The greater part of the embryo above the radicle readily splits into two lobes. These are called the **cotyledons,** and are thick and fleshy because of the large amount of stored food-material which they contain. The cotyledons are in reality special storage leaves.

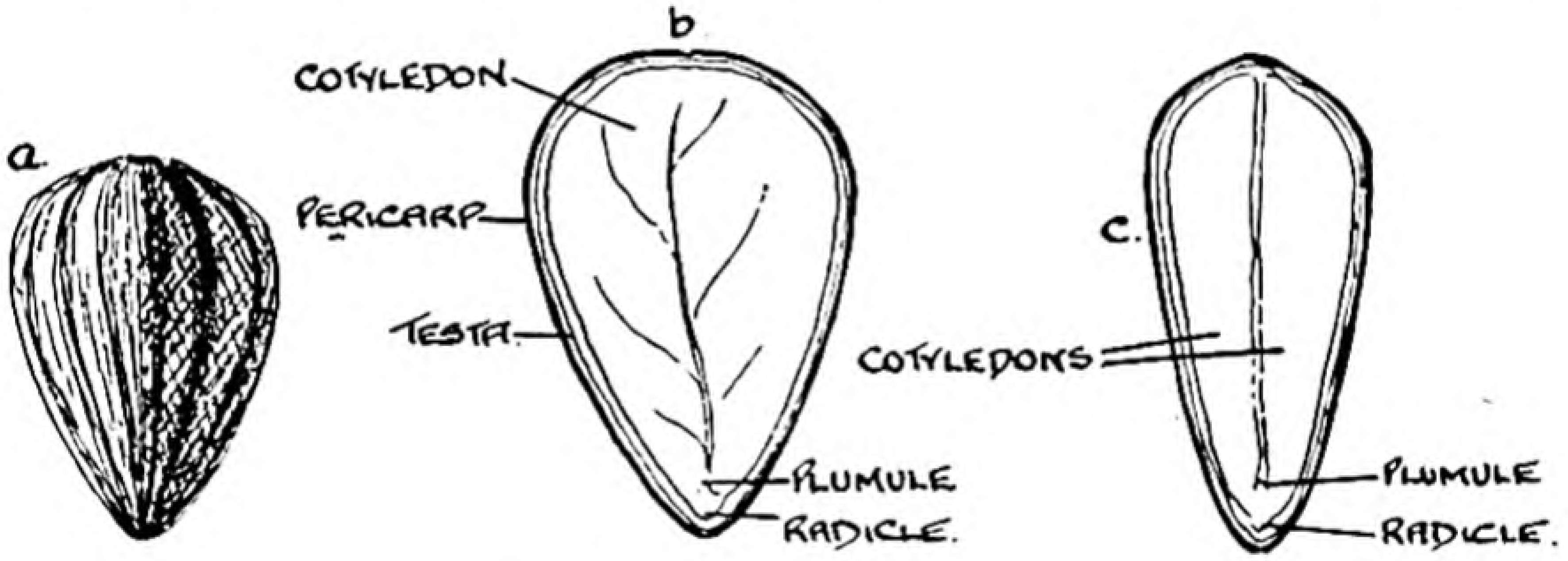


Fig. 38. SUNFLOWER SEED.
A, External; B, Embryo; C, Section at right angles to cotyledons.

If a thin section of a cotyledon is examined under the microscope, the cell-structure can readily be made out. The cells contain aleurone grains and a large amount of oil. If the cotyledons are gently separated there will be found towards the base, and lying between them, a small pointed structure known as the **plumule** which is the growing point of the shoot. The parts of the embryo are also shown in a longitudinal section (Fig. 38, C).

Germination.—If the fruit is placed in the soil, under suitable conditions, the seed begins to *germinate*. Under the term germination are included all changes that take place from the time the dry seed is planted until the resulting young plant establishes itself. In the dry seed the embryo plant is alive, but is said to be dormant. This is not strictly true. In fact, in all the living cells of the dry seed metabolic processes are going on all the time. If they ceased the cells would die. In the dry seed, however all these vital activities proceed only very slowly, and so we can say that the cells are relatively inactive. Germination involves a large and rapid acceleration of the metabolic processes of the cells of the seed.

The process of germination may be conveniently studied if we place sunflower seeds in moist sawdust. The sawdust should be moist and not flooded with water. The first stage in germination is the absorption of water. This takes place quickly and the seed by water absorption may double its weight in twenty-four hours. This water is absorbed by the forces of imbibition and the absorbed water causes a swelling of the embryo, so that the pericarp is burst. This process of water absorption is greatly accelerated by increase in temperature so long as the temperature does not rise above 35°–40° C. At temperatures higher than this, water absorption may be accelerated but the living tissues will be damaged. As water is absorbed by the seed, the rate of the metabolic processes in the cells is increased. Particularly is this true of respiration. It is because of this active respiration, which demands an abundant supply of oxygen, that a good supply of air is necessary if germination is to occur. This is why we sowed the sunflower seeds in moist and not water-logged sawdust. Water-logging would have excluded the air.

The embryo grows and develops into a seedling plant. This takes place at the expense of the food-material stored in the cotyledons. These insoluble substances are first converted by enzymes into soluble compounds. The insoluble proteins are changed to simpler soluble compounds and the oil is probably converted into soluble carbohydrate. These soluble food-materials are translocated to the growing apices of the plumule and radicle. At these points this food-material is built up by the living protoplasm into the substance of the plant, and so new tissues are formed and growth occurs.

During these changes the tip of the radicle first elongates and makes its way out of the fruit. It grows downwards into the soil, and forms the root. The part of the radicle immediately beneath the cotyledons, known as the **hypocotyl,** also elongates, and grows upwards, carrying with it the cotyledons, which increase in size, turn green in the sunlight, and are then readily recognisable as *leaves* of simple form. The *plumule,* which is at first concealed between the cotyledons, eventually develops into the shoot.

When it first appears at the surface of the soil the hypocotyl has the form of a loop or arch. The advantage of this in overcoming the resistance of the overlying soil, and in preserving the plumule and cotyledons from injury, is obvious. The empty fruit-coat may be left behind in the soil, but is usually carried above ground on the tips of the cotyledons. The *hypocotyl* is the portion of the axis which, after germination, lies between the cotyledons and the radicle. It is intermediate in structure between stem and root.

From the above it is evident that the plumule must be regarded as the embryonic *shoot,* the cotyledons as embryonic *leaves,* and the radicle as the embryonic *root.* In the sunflower, as in most seeds, the plumule is an extremely small conical structure, showing no trace of young leaves. In some plants, however, it is large (e.g. almond), and bears little outgrowths which are easily recognised as undeveloped leaves. The axis of a plumule is called the epicotyledonary portion of the axis, or simply the **epicotyl.** Together with the hypocotyl and radicle it forms the axis of the embryo, just as stem and root form the axis of a full-grown plant.

In the sunflower there are two cotyledons. This is characteristic of the Dicotyledons, the group of Angiosperms to which the sunflower belongs. When the cotyledons come above ground and form the first green foliage leaves of the plant, they are said to be **epigeal.**

3. Seed of the Broad Bean

This (Fig. 39) is a true seed, the pod of the bean being the fruit. The seed, as before, should be soaked in water, so that the **testa** or seed-coat may be removed easily. On the testa at one end of the seed there is an elongated scar of a dark colour, the **hilum.** This is the point where the seed has broken away from its stalk. On gently pressing the soaked seed, a drop of moisture will be seen to exude from a minute aperture—the **micropyle**—situated at one end of the hilum. Hilum and micropyle are also present, but not easily recognisable in the sunflower, because they belong to the testa and are covered by the pericarp.

Inside the seed-coat there is a large embryo plant. This consists, as in the sunflower, of a radicle, a plumule, and two cotyledons. The **radicle,** which is to one side, lying in a little pocket formed by the seed-coat, is short and blunt. Its tip lies close to the micropyle. The **cotyledons** here are much more massive than in the sunflower, because of the larger amount of food-material stored in them. The food-material consists of starch and protein grains. The **plumule,** as in the sunflower, lies between the cotyledons. It is, however, larger, and shows the rudiments of young leaves.

During germination of the broad bean the hypocotyl remains short and the cotyledons remain underground, gradually giving up their stored food-materials to the developing plumule and radicle. They are said to be **hypogeal.** Their leaf-character is shown by the fact that buds form in their axils and may give rise to aerial shoots, especially if the plumular shoot is injured. The lowest internode of the epicotyl remains arched, with the plumular bud bent backwards, until it emerges from the soil, when it straightens out. The plumular shoot then proceeds to develop, producing a series of leaves of increasing complexity of form, the later formed leaves being compound and pinnate; the rachis, terminating in a point, bears one or more pairs of leaflets and at the base of the petiole is a pair of stipules.

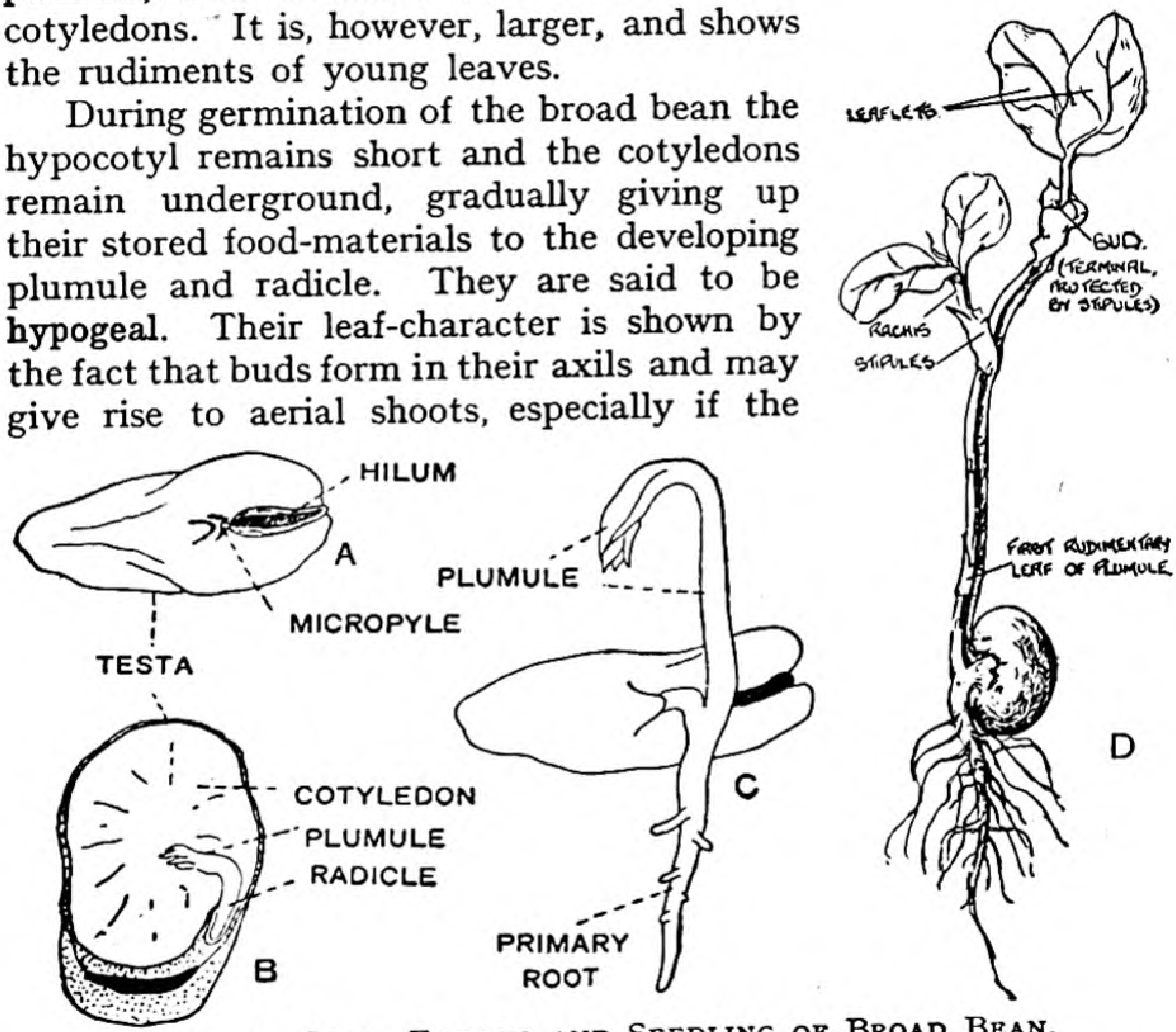


Fig. 39. SEED, EMBRYO AND SEEDLING OF BROAD BEAN.

The French or kidney bean (*Phaseolus vulgaris*) and the scarlet runner (*Phaseolus multiflorus*) are closely allied to the broad bean

(*Vicia faba*). The structure and germination of the seed of the broad bean may also be compared to those of other of its allies, e.g. French bean, Lima bean (*Phaseolus lunatus*), gram (*Cicer arietinum*), lablab (*Dolichos Lablab*) and crab's eye (*Abrus precatorius*), in which the cotyledons are epigeal, and to ground nut (*Arachis hypogoea*), pea (*Pisum sativum*) and scarlet runner where they are hypogeal.

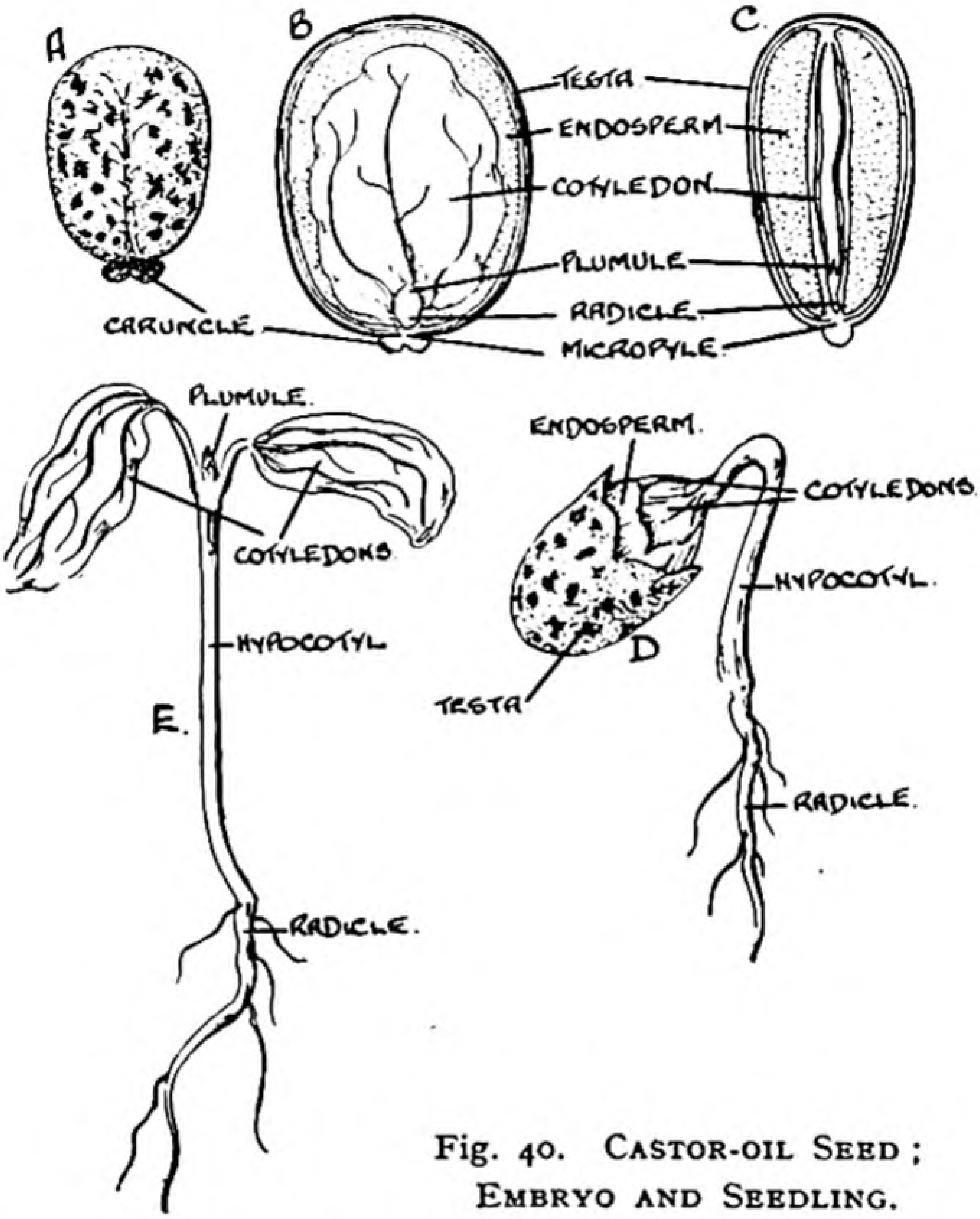

A
B
C
TESTA
ENDOSPERM
COTYLEDON
PLUMULE
RADICLE
CARUNCLE
MICROPYLE
PLUMULE
ENDOSPERM
COTYLEDONS
COTYLEDONS
HYPOCOTYL
HYPOCOTYL
D
TESTA
E.
RADICLE
RADICLE

Fig. 40. Castor-oil Seed; Embryo and Seedling.

14. Castor-oil Seed (Fig. 40)

Seeds of the castor-oil plant (*Ricinus communis*) are from 8 to 15 mm. long, and have a smooth, glossy, brittle testa which may be greyish-brown or mottled reddish-brown. At one end is a pale, whitish *caruncle* which can be removed, showing, underneath, the hilum which is a darkish spot, and the micropyle to one side of it. From the caruncle, along the ventral (flattish) surface, runs a distinct line (the *raphe*) which divides at a slightly raised point (the *chalaza*) near the opposite end. The dorsal surface is somewhat rounded. When the testa is removed, the kernel is seen to be covered with a thin, papery *tegmen*. The rest of the kernel consists of an oily, yellowish-white *endosperm* enclosing the embryo. If the endosperm is carefully slit round the edge, and the two halves broken apart in the flat plane, the two cotyledons are seen as rudimentary leaves in which palmate venation can be distinguished, their dorsal (lower) surfaces appressed to the solid endosperm. The radicle is a peg-like structure at the micropylar end of the endosperm, and the plumule is so minute as to be hardly distinguishable at this stage, but it lies between the two cotyledons. The reserve food-material is stored in the endosperm in the form of oil and aleurone grains (Fig. 14).

Thus in the seed of castor-oil plant the food-material is contained in a special tissue in which the embryo is embedded. Seeds of this kind are called **albuminous** or **endospermous.** In the sunflower and bean food-substance is also stored, but it is in the cotyledons, and not in a special endosperm tissue. Such seeds are **exalbuminous** or **non-endospermous.**

In the process of germination the cotyledons remain for some time inside the seed. They absorb the food-material in the endosperm and increase in size. Owing to the elongation of the hypocotyl the seed is carried above ground and the cotyledons form the first green leaves. As in sunflower the hypocotyl is bent or arched when it reaches the surface of the soil. An interesting feature of the expanded, green cotyledons is that they have extra-floral nectaries where the lamina joins the petiole.

5. **Maize** (Fig. 41)

The so-called maize (Indian corn) seed is really the fruit (caryopsis) of *Zea mays*, a member of the grass family. *Pericarp* and *testa* are both thin, and fused together to form a single membrane. The grains of the " White Horsetooth " variety are larger and more regular in shape than those of the ordinary " Indian corn," and are therefore better for purposes of study. The seeds may be softened before examination by soaking them in water for some time.

On one side of the fruit there is an oblong area of a lighter colour (Fig. 41, A). This is the embryo; the rest is the endosperm. On the same side of the fruit as the embryo, in the middle, near the broad end, is a projecting point, the remains of the stigma, which shows that the outer covering is the pericarp, and that we are dealing with a fruit. If the fruit is cut longitudinally through the middle of this area, the embryo will be seen in section lying to one side of a mass of endosperm (Fig. 41, B). When the cut surface is moistened with iodine solution, the endosperm is stained blue, and is thus shown to be rich in starch. In microscopic sections, however, it is found that the outermost layer of the endosperm, the layer lying just under the testa, contains aleurone grains; it is called the **aleurone layer.**

The embryo consists of a large *plumule*, a *radicle*, and a structure called the **scutellum.** The embryo can be dissected away from the endosperm, thus exposing the surface of the scutellum in contact with the endosperm. A median longitudinal section of the embryo in the plane at right angles to the surface of the scutellum, when viewed under the microscope, shows the plumule and radicle each covered by a sheath, the **coleoptile** and the **coleorhiza** respectively, whilst a **ligule** projects laterally. The morphology of these organs has been the subject of much discussion, their interpretation being based on possible homology and on comparative anatomy. Without going into the details of the arguments for and against, there are those who hold the view that the scutellum and coleoptile represent parts of a single cotyledon, whilst others regard the scutellum as the cotyledon and the coleoptile as the first plumular leaf.

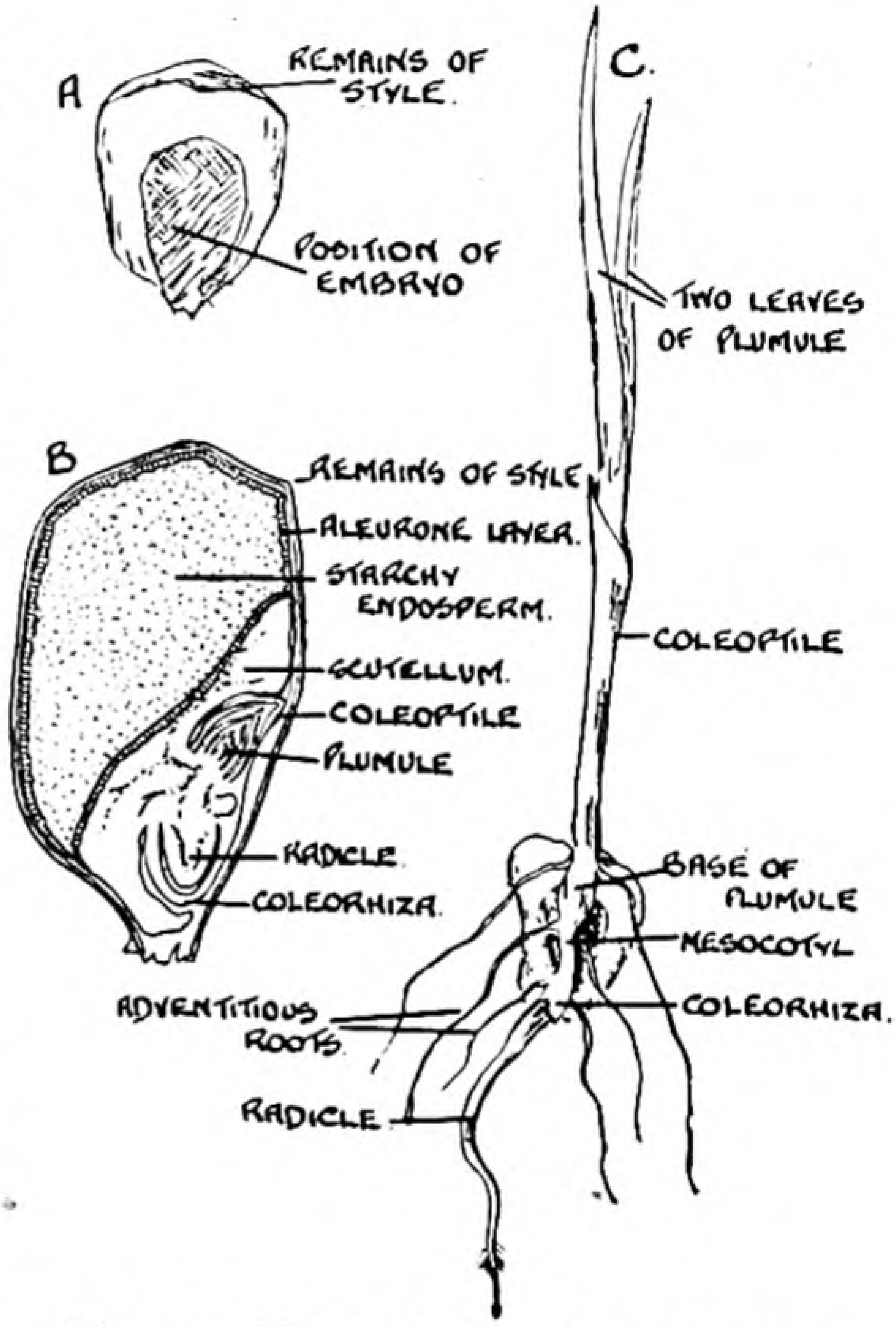

A
REMAINS OF STYLE.
POSITION OF EMBRYO
C.
TWO LEAVES OF PLUMULE
B
REMAINS OF STYLE
ALEURONE LAYER.
STARCHY ENDOSPERM.
SCUTELLUM.
COLEOPTILE
PLUMULE
RADICLE
COLEORHIZA.
COLEOPTILE
BASE OF PLUMULE
MESOCOTYL
COLEORHIZA.
ADVENTITIOUS ROOTS.
RADICLE

Fig. 41. MAIZE GRAIN AND SEEDLING.
A, External; B, L.S. through embryo; C, Seedling.

During germination the scutellum secretes enzymes which convert the starch and protein of the endosperm into soluble substances. These pass into the embryo through the scutellum and are used in the growth of the plumule and radicle. The coleoptile emerges above ground by its own growth and also by the elongation of the region between its base and the attachment of the scutellum. This region is called the *mesocotyl* by those who view the scutellum and coleoptile as parts of one cotyledon. In this case the mesocotyl is the elongated cotyledonary node. According to the other view, it is the first internode of the epicotyl. The scutellum remains below ground, and the plumular leaves emerge from the tip of the coleoptile, which remains relatively small. These leaves have a sheathing base, a flat, strap-shaped lamina with parallel venation (another feature of Monocotyledons) and a membranous ligule where the lamina joins the sheath. The successive nodes, where the bases of the sheaths join the main stem, remain close together near ground-level, during the early development of the shoot, but later, when the inflorescence is developing, they become separated by distinct internodes.

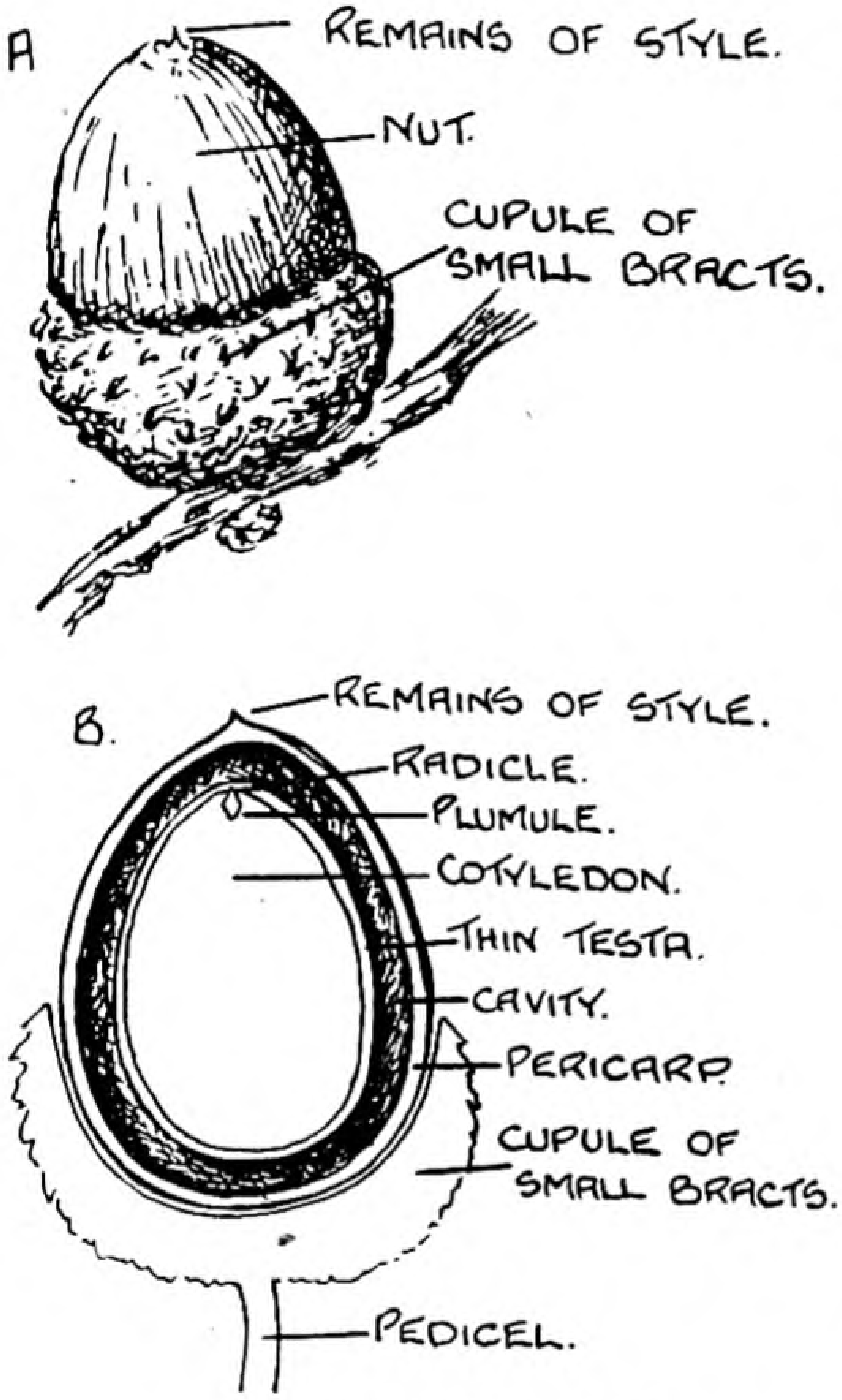


Fig. 42. Fruit of Oak.

A, External Features; B, L.S. in plane of cotyledons.

The coleorhiza swells somewhat, but the radicle soon penetrates through it into the soil and may give off lateral roots. These do not, however, give rise to the main root-system of the plant. This arises from adventitious roots which are formed firstly from the base of the coleoptile and later from the succession of closely placed nodes at the base of the shoot. Such a root-system forms a fibrous root.

Branching of the shoot may take place from axillary buds which arise, one at each node, between the base of the leaf-sheath and the main shoot.

Maize belongs to the large and economically important family of grasses (Gramineae). The " seeds " of wheat, barley and oat are similar to maize in structure and germination, and should be studied and compared with it.

6. Notes on Other Seeds

The four seeds described above may be regarded as examples of the more important types of seed. The following, which are considered more briefly, should be compared with them:—

Oak (Fig. 42).—The nut or acorn of oak (*Quercus Robur*) is a fruit. The cup in which it is seated is called the *cupule*. The nut may contain several seeds, but usually there is only one. The seed is exalbuminous. The two cotyledons, which are closely pressed together and can only be separated with some difficulty, are large and massive. The plumule and radicle are both small and lie at the pointed end of the seed. They can be recognised by separating the cotyledons, but are best seen in a longitudinal section. The cotyledons are hypogeal.

Gourd (*Cucurbita*, Fig. 43).—The seed is flat but with a thickened margin. It is non-endospermous, and in the two somewhat fleshy cotyledons veins are usually evident. When wet the testa is sticky, and this helps to anchor the seed to moist soil. Radicle and plumule are both relatively short and thick. Owing to its shape the seed generally lies flat on the soil, and when germination begins the radicle protrudes between the halves of the testa and grows down into the soil at right-angles to the seed. Very soon a small peg develops in the angle between the vertical radicle and the still horizontal hypocotyl. The peg tends to hold down the lower half of the seed-coat, whilst the upper half is raised by the arching of the hypocotyl which eventually carries the cotyledons out of the seed-coat and becomes erect.

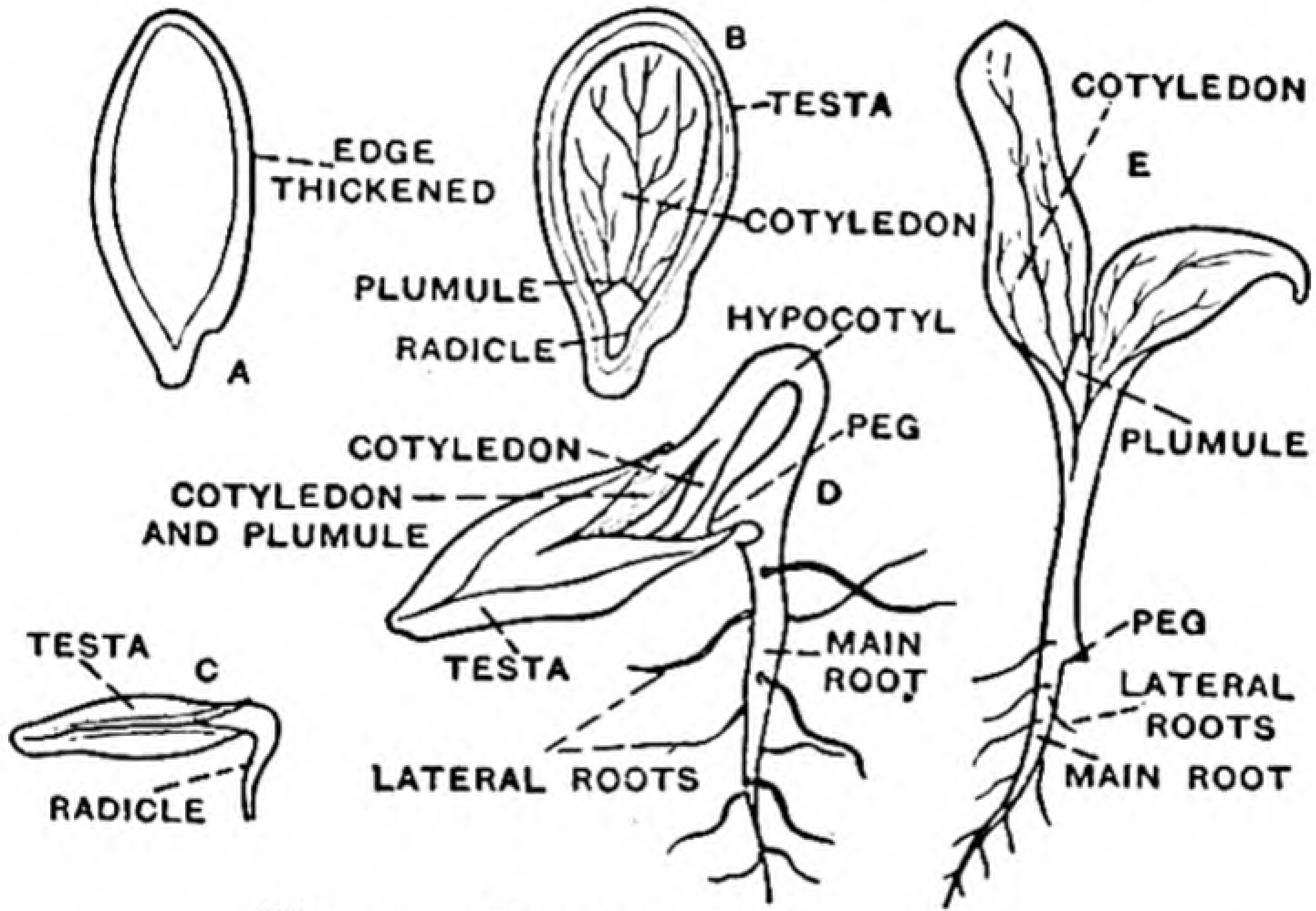


Fig. 43. GERMINATION OF GOURD.
A, Seed. B, Seed with one cotyledon removed. C, Beginning of germination. D, E, Further stages.

Coffee (*Coffea arabica*, Fig. 44 A-C).—Two seeds are enclosed in a scarlet berry-like fruit, known as "the cherry." They are flattened, each with a longitudinal groove on the sides facing one another and enclosed in mucilaginous material. The seed consists chiefly of hard horny endosperm with the small embryo embedded in its lower end, on the side remote from the groove. The food reserve is largely in the form of hemicellulose (see p. 30), deposited as thickening on the walls of the endosperm cells, and if the endosperm is carefully shaved away the embryo with its two small cotyledons becomes visible. The cotyledons are epigeal and germination is slow, extending over several weeks.

Jak (*Artocarpus integrifolia*, Fig. 44, D).—The jak fruit is composite, being derived from a whole inflorescence. The seeds are numerous and embedded in a fleshy pulp. The brown seed-coat shows two distinct layers and inside this testa is the non-endospermous seed. The two cotyledons are unequal in size and are laticiferous, exuding latex when cut. The cotyledons are hypogeal but, although they never come above the ground, they develop a green colour.

Brazil Nut (*Bertholletia excelsa*).—In this seed the hard shell is the seed-coat. The seed is non-endospermous. The cotyledons and plumule are very minute and occupy the broader end of the embryo. The radicle is also very small and lies at the narrow end. The greater part of the embryo consists of the swollen *hypocotyl*, whose cells contain oil and protein grains.

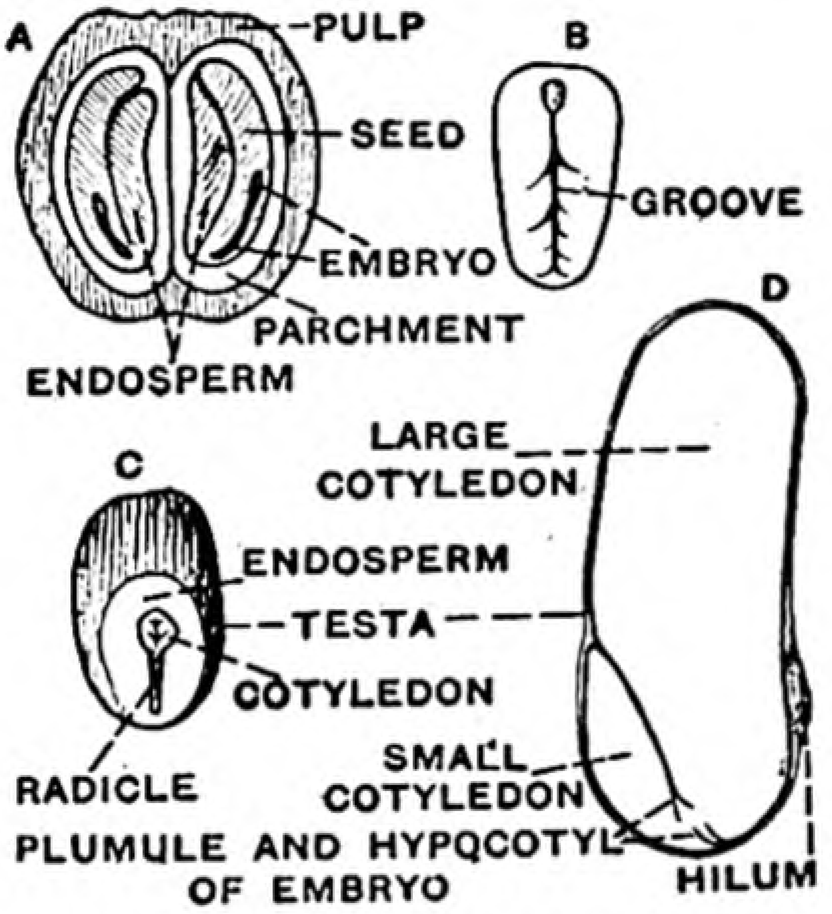


Fig. 44. Coffee and Jak.
A, Coffee fruit cut in half. B and C, Seed of Coffee; in C, endosperm cut away, exposing embryo. D, Seed of Jak, cut in half.

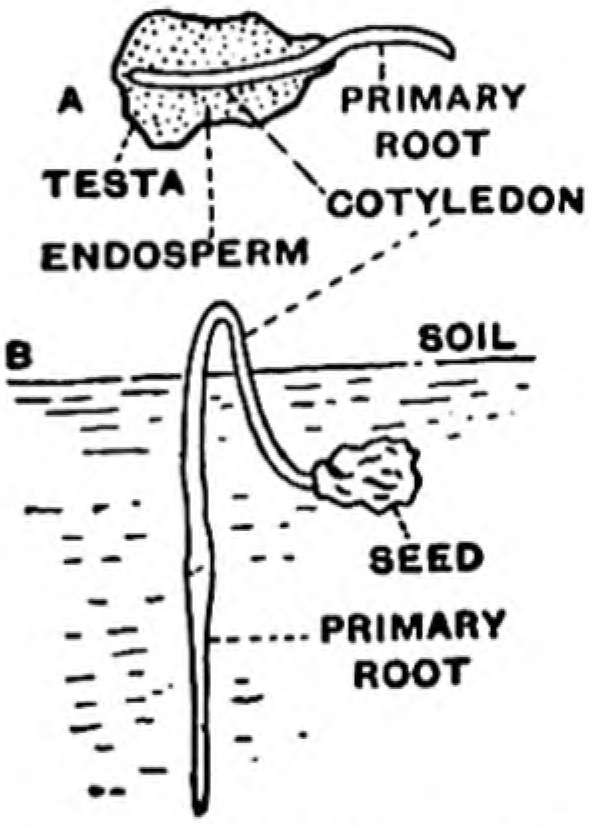


Fig. 45. Germination of Onion.

Onion (*Allium cepa*, Fig. 45).—The small black seeds are very irregular in shape, but are somewhat pointed at the base where the seed was attached to the fruit. Before examination the seed should be soaked in water to soften it. A longitudinal section should show a somewhat slender curved embryo embedded in endosperm. The radicle is towards the pointed base of the seed; towards the other end is the single cotyledon. The plumule is small and is concealed within the base of the hollow cotyledon.

At germination the radicle elongates and grows down into the soil as the first root, but afterwards, as in the maize, its place is taken by roots developed from the base of the stem. The lower part of the cotyledon also elongates and grows out of the seed-coat. Bent over so as to form a loop or arch like the hypocotyl of the sunflower, it passes above ground and forms the first green foliage leaf. The tip of the cotyledon, however, remains coiled up inside the seed-coat and absorbs the endosperm. At a later stage a second leaf, developed from the plumule, bursts through the base of the cotyledon and comes above ground.

Date (*Phoenix dactylifera*, Fig. 46).—The familiar date "stone" is the seed. The brown outer layer is the seed-coat. Along one side there is a deep groove or furrow. In the middle of the other side a little protuberance will be observed, which marks the position of the embryo. If the "stone" is cut transversely at this point, the small embryo will be seen embedded in hard, horny endosperm. The hardness of the endosperm is due to the thickness of the cell-walls, which represent a store of carbohydrate food-material in the form of cellulose (Fig. 16, A).

The process of germination can be studied if the stone is put in moist sawdust or soil and kept sufficiently warm. The pointed radicle elongates, grows down into the soil, and forms the primary root. The lower part (sheath and stalk) of the single cotyledon also grows out of the seed, but the upper part remains inside the seed and absorbs the endosperm. The cellulose is gradually converted into sugar by means of an enzyme secreted by the cotyledon. The primary root branches, and is more strongly developed than is usual in Monocotyledons, but it does not give rise to the root-system of the plant. The plumule is enclosed in the sheath of the cotyledon; it bears leaves, which eventually break through the sheath and come above ground.

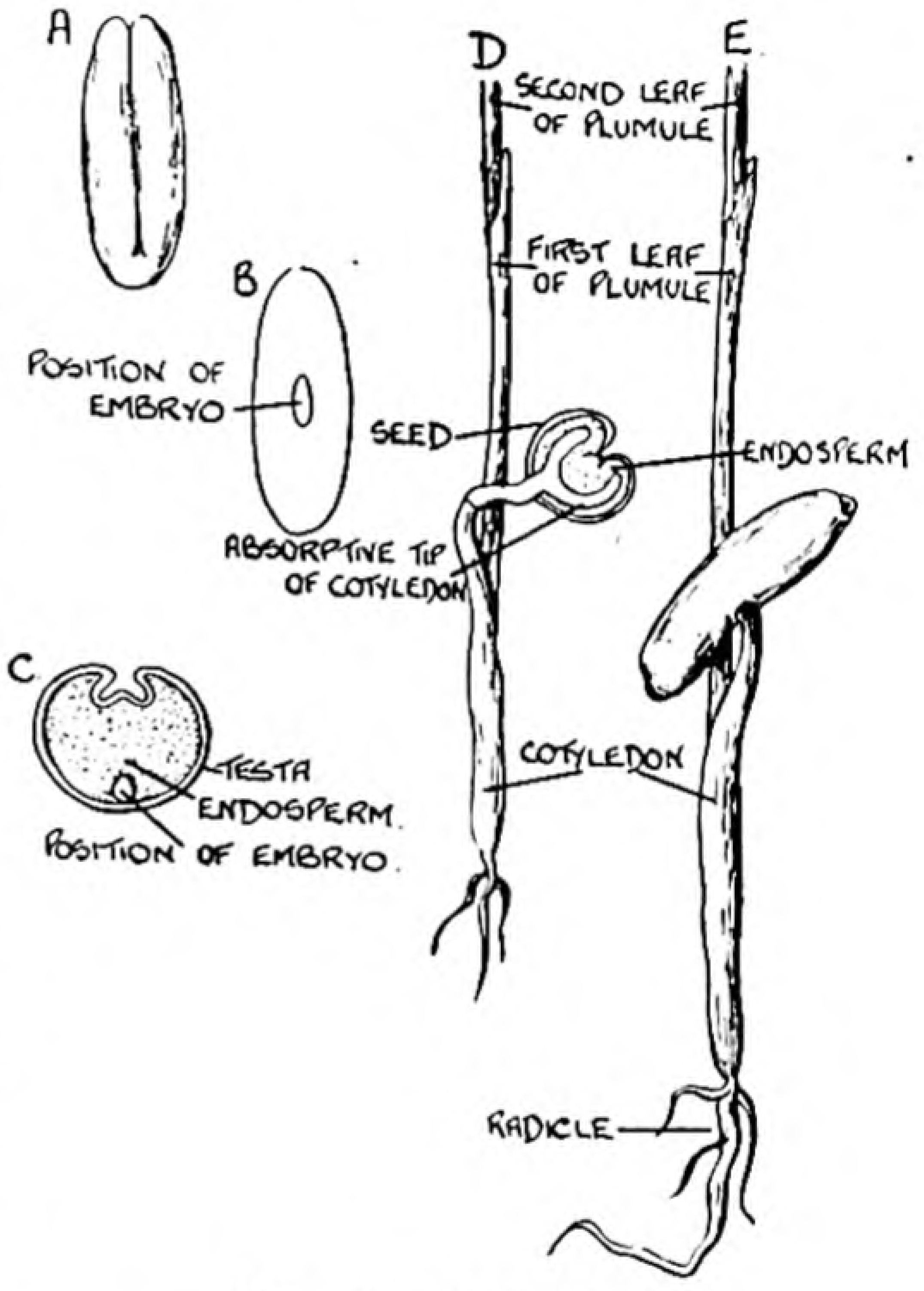


Fig. 46. DATE SEED.

A, External; B, T.S. through embryo; C, Seedling.

Canna (*Canna indica*).—The monocotyledonous seed of this plant has a small straight embryo with a short, rounded cotyledon. Food material is stored in both endosperm and persiperm and passes to the developing seedling *via* the cotyledon, which functions here very much like the cotyledon of the date.

✓7. Monocotyledonous and Dicotyledonous Seeds

(A) DICOTYLEDONS.—The embryo has almost invariably two cotyledons. In exceptional cases there may be three (e.g. occasionally in sycamore and oak) or only one (e.g. some

Ranunculaceae). The seeds in most Dicotyledons are exalbuminous. If the cotyledons are small and contain a relatively small amount of food-material, e.g. in cress and mustard, it is evidently necessary that the seedling should establish itself as quickly as possible. In this case the radicle elongates rapidly and the cotyledons and plumule are quickly carried above ground by the elongation of the hypocotyl. It is only in some seeds, where the cotyledons are very large, that the latter remain inside the seed-coat, *i.e.* are hypogeal.

There are, however, many examples of albuminous seeds, e.g. in plants belonging to the families Ranunculaceae and Umbelliferae. The amount of endosperm varies. Sometimes it is abundant, and the embryo very small. In other cases, e.g. in Labiatae, it is reduced to a thin layer and the embryo is relatively large. The relation of the embryo to the endosperm also varies. It may, for example, be embedded in the endosperm, or may be coiled round it. But in all cases the tip of the radicle lies close to one side, near the micropyle. In albuminous seeds the cotyledons remain inside the seed till the endosperm is absorbed and then form the first green leaves.

Typically in Dicotyledons the primary root persists and forms the root-system of the plant.

(B) MONOCOTYLEDONS.—The embryo, as already indicated, has only one cotyledon. The seeds of orchids and of many aquatic Monocotyledons are exalbuminous; but the great majority of monocotyledonous plants have albuminous seeds.

The cotyledon may come above ground as the first foliage leaf, as in the onion. In most cases, however, it is hypogeal, either the whole of it, or its upper part, remaining behind in the seed and absorbing the endosperm. Usually the radicle and plumule are pushed out of the seed by the downward growth of the lower part of the cotyledon. The plumule may be large, as in grasses (e.g. maize); but it is usually very small, and, as a rule, concealed within the base of the cotyledon. The primary root, although it may develop fairly strongly at germination, is soon replaced by other roots developed from the base of the stem.

8. Uses of Cotyledons

The seeds examined show how diverse may be the functions of the cotyledons. They are nearly always concerned with the nutrition of the embryo plant. In non-endospermous seeds they contain a store of food-material, and in some cases, e.g. broad bean, they are little more than stores of food. In endospermous seeds they function as absorbing organs. They secrete the enzymes which convert insoluble stored substances into soluble compounds; they absorb these soluble compounds and then pass them on to the developing plumule and radicle. Finally, in many plants the cotyledons come above the ground, form the first green foliage leaves and become active in synthesising new food-material by the process of photosynthesis. Cotyledons, even when they become the first green leaves, have a much simpler form than the foliage leaves which follow them.

9. Examination of Seeds

In examining seeds the student should endeavour to find out the following points:—(*a*) whether dicotyledonous or monocotyledonous, (*b*) whether endospermous or non-endospermous, (*c*) the position, form and size of the embryo, (*d*) the nature and distribution of the food reserves, (*e*) the external characters of the seed-coat. In large seeds dissection and observation with a hand lens yield information on some of these points. With the smaller seeds recourse must be had to microscopic examination of their sections.

The application of microchemical tests to thin sections will reveal the nature and distribution of the food-reserves. The substances most likely to be found as food-reserves are hemicellulose, starch, oil and protein. In this connexion it may be pointed out that seeds containing much oil or fat rarely contain more than a trace of starch.

If the seed is tested for food-reserves during germination, the gradual disappearance of food-materials from the seed can be traced. To study germination seeds may be planted in moist sawdust or coconut fibre and removed periodically for examination. A convenient plan is to replace one side of a box with a sheet of glass, fill the box with moist sawdust and sow the seeds close to the glass so that they may be readily observed. When this plan is followed the germinating seeds should not be permanently exposed to the light. The glass sheet should be covered externally with a piece of black paper which can be removed from time to time in order to examine the germinating seeds. The reason for shading the seeds is not obvious. In the case of maize the plumule bursts through the coleoptile when the seedling is exposed to light on reaching the surface of the soil. Permanent illumination would result in an abnormally early rupture of the coleoptile. In a broad bean seedling the hooked plumule straightens only when it comes above ground. Unless the germinating seed is shaded, premature straightening of the plumule may occur, so that an incorrect picture of the process of germination is obtained.

CHAPTER IV

THE STEM OF THE ANGIOSPERM

1. The stem and leaf structures into which the shoot in the Angiosperm is differentiated show an immense variety of forms. For this reason it will be convenient to study them separately. The present chapter is therefore devoted to the stem—its general external characters and internal structure.

A. External Characters

2. Nodes and Internodes

We have already stated that the plumule grows upwards into the light, and develops into the shoot of the plant. This consists of the main stem bearing leaves, and also branches (lateral stems) bearing leaves. In the fully grown part of most stems, the leaves are separated by intervals from each other. The points at which one or more leaves are given off are called the **nodes** of the stem, and the regions between these the **internodes** (Fig. 47).

3. General Descriptive Terms

Usually stems in transverse section are circular, and are described as **cylindrical.** Others are marked by alternate ridges and furrows. and are said to be **angular.** Thus the stems of most Labiatae are quadrangular or " square." Some stems are flattened. In rarer cases we meet with globular or altogether irregular stems. The stem may be either **herbaceous** or **woody.** In some plants, as in wallflower, it is herbaceous above and woody below. Some herbaceous stems are more or less dilated or expanded at the nodes. This is due to the arrangement of vascular tissue at these points. The stems appear jointed, and hence the term **jointed** or **articulated** is applied to them. Examples are met with in grasses. The stem may be more or less **hairy.** It may be **prickly** or **spiny.** If there are no hairs, and the stem is quite smooth, it is described as **glabrous**; if, in addition, it is more or less sea-green or covered with a bluish "bloom," it is said to be **glaucous.**

4. Buds (Fig. 48)

The growth in length of the main stem, or a branch, takes place mainly towards the apex. At the extreme apex the internodes have not yet elongated; the young leaves, which are in the course of development, are crowded together and closely overlap the growing apex

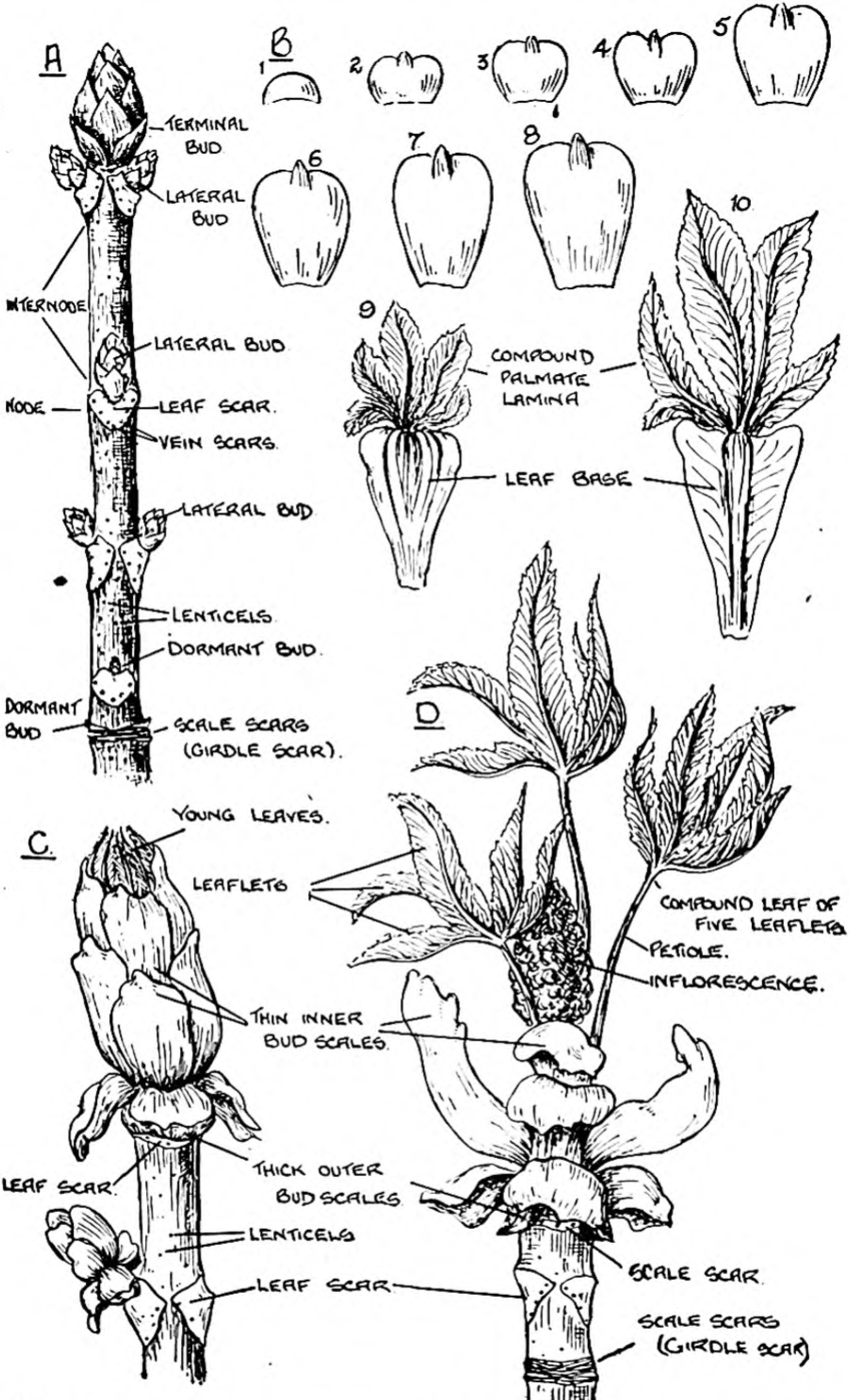

A
TERMINAL BUD
LATERAL BUD
INTERNODE
LATERAL BUD
NODE
LEAF SCAR.
VEIN SCARS.
LATERAL BUD
LENTICELS
DORMANT BUD.
DORMANT BUD
SCALE SCARS (GIRDLE SCAR).
B
1
2
3
4
5
6
7
8
9
10
COMPOUND PALMATE LAMINA
LEAF BASE
C.
YOUNG LEAVES.
LEAFLETS
THIN INNER BUD SCALES.
THICK OUTER BUD SCALES
LEAF SCAR.
LENTICELS
LEAF SCAR
D
COMPOUND LEAF OF FIVE LEAFLETS
PETIOLE.
INFLORESCENCE.
SCALE SCAR
SCALE SCARS (GIRDLE SCAR)

Fig. 47. A, Twig of Horse-chestnut; B, Terminal Bud Dissected to show Transition from Bud Scales to Foliage Leaves; C, Bursting Bud; D, Opened Bud.

of the stem or branch. This compact structure, which we nearly always find at the apex of a stem, is called a **terminal** bud. As growth takes place the internodes gradually elongate, and the leaves become separated.

It is important to notice that the branches of a stem make their first appearance as buds. These buds, which, with reference to the stem on which they are borne, are called **lateral** buds, are situated in the **axils** of the leaves, *i.e.* in the angle between the leaf and the upper part of the stem. The *axillary* position of the buds should be carefully noticed. In the Angiosperms it is the rule that each leaf has a bud in its axil.

Very frequently, either naturally or owing to the influence of external conditions, only some of these buds develop into branches; the others remain dormant. In circumstances of necessity, however, as, for example, when the main stem and chief branches have been destroyed, these **dormant** buds become active, and give rise to *deferred shoots*. Sometimes the shoots developed late on the stems of trees have this character.

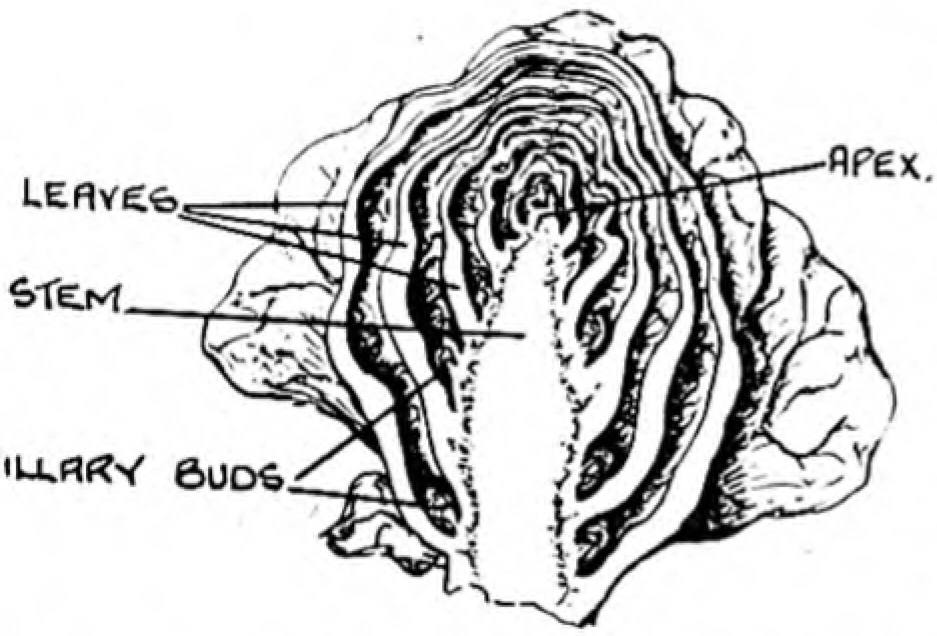


Fig. 48. BRUSSELS SPROUT CUT LONGITUDINALLY.

A **bud**, then, as found in Seed Plants, may be defined as a rudimentary or embryonic shoot, consisting of a short axis in which the internodes have not yet elongated and in which the young leaves are closely crowded together and overlap the apex. These buds can be recognised on plants at all seasons, but are most noticeable in winter.

In many buds the young leaves are all of the same kind and in course of time develop into green foliage leaves, but in most winter buds only the central leaves of the bud are of this kind, while the outer ones are small and scaly—*scale-leaves*—and serve as a protection against cold and loss of water (Fig. 47). In those regions of the tropics where there is a regular alternation of dry and wet seasons many buds are similarly protected by bud-scales during the dry period. In many buds the loss of moisture, which would be injurious to them, is more effectually prevented by the corky nature of the scales, by the secretion of mucilaginous or resinous substances (e.g. *Aesculus indicus*), or by the development of a covering of hair, as in the jujube tree (*Zizyphus*).

When the buds unfold in spring the bud-scales fall off and leave a zone or girdle of close-set scars. The age of any particular branch can be determined by counting the number of these zones between its base and apex. They are well seen in pipul (*Ficus religiosa*) and kapok (*Eriodendron*).

The **normal** axillary buds are developed in acropetal order (p. 7). Buds which are developed out of their proper order, or without any relation to the leaves, are called **adventitious.** The shoots of pollards and those developed on the trunks of many trees (e.g. jak) arise from such buds. They may also be developed on leaves or roots. If the leaf of *Begonia,* for example, is artificially wounded and laid on the surface of the soil, adventitious buds are developed from the wounded surface and produce new plants. Buds occasionally arise naturally on the succulent leaves of *Bryophyllum pinnatum.* Adventitious buds commonly spring from the root in dandelion, rose, hazel, silver wattle (*Acacia dealbata*) and coffee.

Sometimes more buds than one are developed in the axil of a leaf. These are called **accessory** buds. Examples are found in the walnut, *Fuchsia, Capparis* and *Aristolochia.*

5. Branching of the Stem

The branching of the stem in Angiosperms is probably always **lateral** (p. 7); in other words, the branches arise as lateral buds in the axils of the leaves. The young leaves and their axillary buds originate as little protuberant outgrowths just below the extreme tip of the parent-axis. The branching may be **racemose** or **cymose** (p. 7.)

In indefinite racemose, or monopodial branching (Fig. 3, B) there may be, at each node, either a single branch or a series (called a **whorl**) of two or more branches, according to the number of buds developed (which will depend largely on the number of leaves). Definite or cymose branching, if only one daughter-axis is given off at each branching, is said to be **uniparous** (Fig. 49, A and B); if two, **biparous** (Fig. 49, C); if more than two **multiparous.** The biparous cymose form of branching, or dichasial cyme, owing to the abortion of the growing-point of the parent-axis, frequently resembles a dichotomy, hence the name *false dichotomy* is often applied to it. Examples are seen in mistletoe and some cacti.

In uniparous cymose forms the successive daughter-axes may be developed right and left alternately—the cincinnus (Fig. 49, A); or always on the same side—the bostryx (Fig. 49, B). In these two forms the branching would present a zigzag or spirally coiled appearance respectively, if the branches retained the position in which they are developed. But in nature the branching usually becomes straightened out (Fig. 49, A*c*, B*c*), and the basal portions of the successive daughter-axes constitute what *to all appearance* is a simple parent-axis, but is *really* a false axis or **sympodium.** The cincinnus resembles a typical raceme; the bostryx a one-sided raceme. These *sympodial* forms are distinguished from true monopodial ones by the position of the leaves, which, it should be noticed, are given off on the opposite side from what are *apparently* lateral branches. (Contrast Fig. 3, B.)

The student is advised to make a careful practical study of branching by examination of a number of plants. The monopodial form is the commoner in vegetative parts of stems; but sympodial growth is frequently met with in trees—e.g. the uniparous form in beech, elm, and lime, where, owing to the death of the terminal bud at the end of the year, the growth in the following year is continued by a lateral bud. Modifications of the biparous form are seen in members of the family Solanaceae, such as *Datura Stramonium*, and *Atropa Belladonna* (Fig. 50, A and B). The latter appears to be uniparous (a cincinnus).

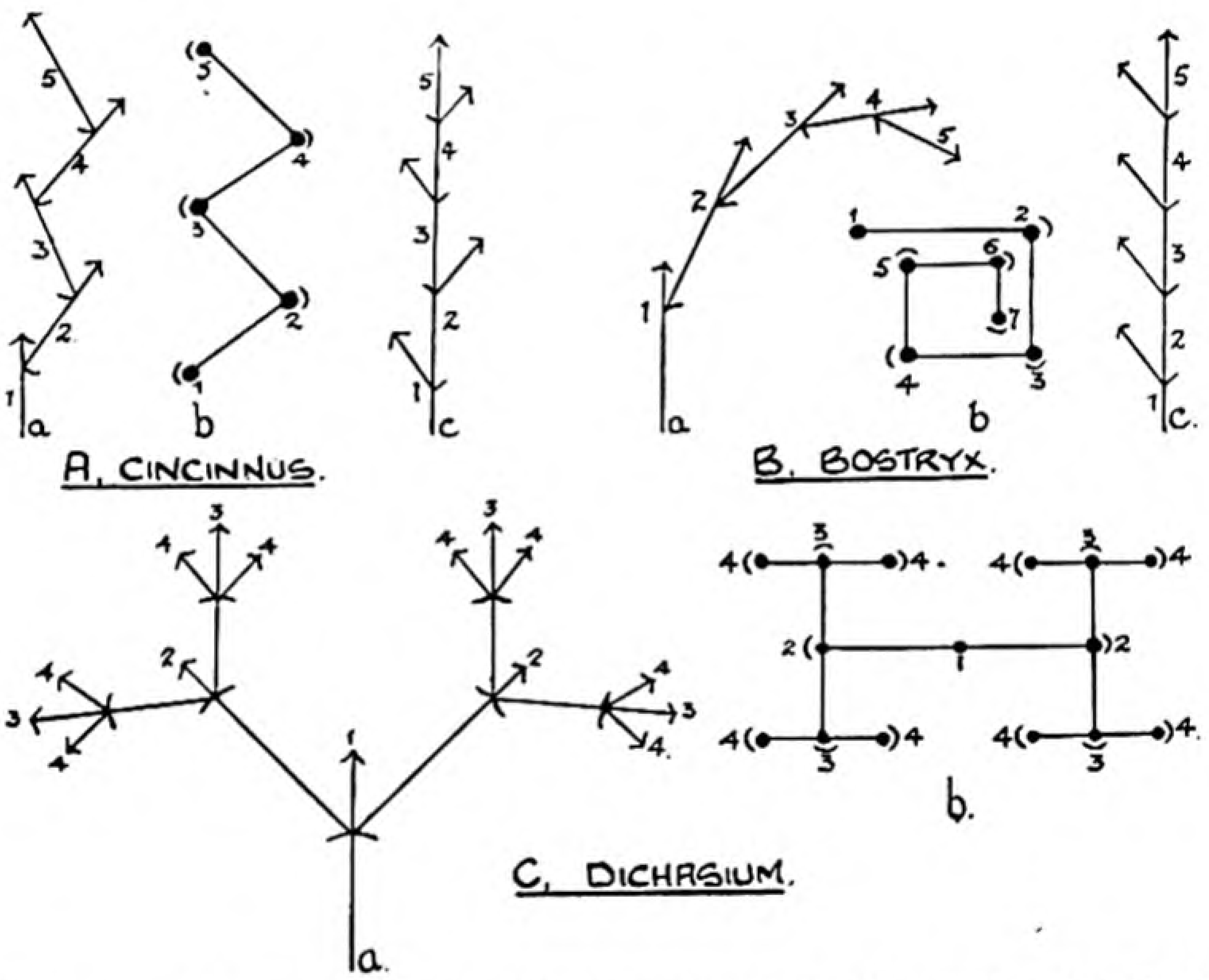


Fig. 49. Forms of Cymose Branching in Profile and Plan.
A and B, Uniparous; C, Biparous; *a*, Theoretical, *c*, Actual, profile; *b*, Plan.

6. Forms of Stems

We have already indicated that the form and structure of the various parts of the plant can be related to the functions which they perform. Ordinarily stems bear foliage leaves, and in such a way that the leaves are exposed to light and enabled to function as organs of photosynthesis. Stems also serve as conducting channels through which materials synthesised in the aerial parts of the plant may be translocated to roots or other underground organs, and by means of which substances absorbed by the roots from the soil can be transported to the leaves.

Stems, however, may exhibit various degrees of specialisation of form, correlated with special functions which they have assumed. They may be underground instead of aerial, prostrate instead of erect, serve as organs of perennation and as storage organs.

It will be readily understood, therefore, that stem structures assume an immense variety of forms. Some grow *erect* and are self-supporting. Examples of erect stems are sunflower, broad bean, foxglove, in fact, this is the typical form of stem. Erect stems may be woody or herbaceous. Herbaceous stems live generally only for a single growing season, whereas woody stems persist from year to year. Plants with herbaceous stems may be annuals, completing their life-history in a single season; others are biennial, usually growing and forming shoots in one season and producing flowers, fruits and seeds in the second year, death occurring after seed production. Herbaceous perennials have an underground, permanent stem which each year produces a crop of aerial stems which bear foliage leaves and flowers. These aerial stems are short-lived—dying down at the end of the season. Woody stems are generally perennials. Not only are the plants long-lived, but the shoots also are perennial in character. In some woody plants many shoots arise which appear capable of only very limited growth. Such dwarf shoots occur in the jak, where they bear the flowers. Sometimes, for reasons not fully understood, a dwarf shoot or spur may assume the power of rapid and extensive elongation. Extremely short stems occur, too, in many herbaceous perennials.

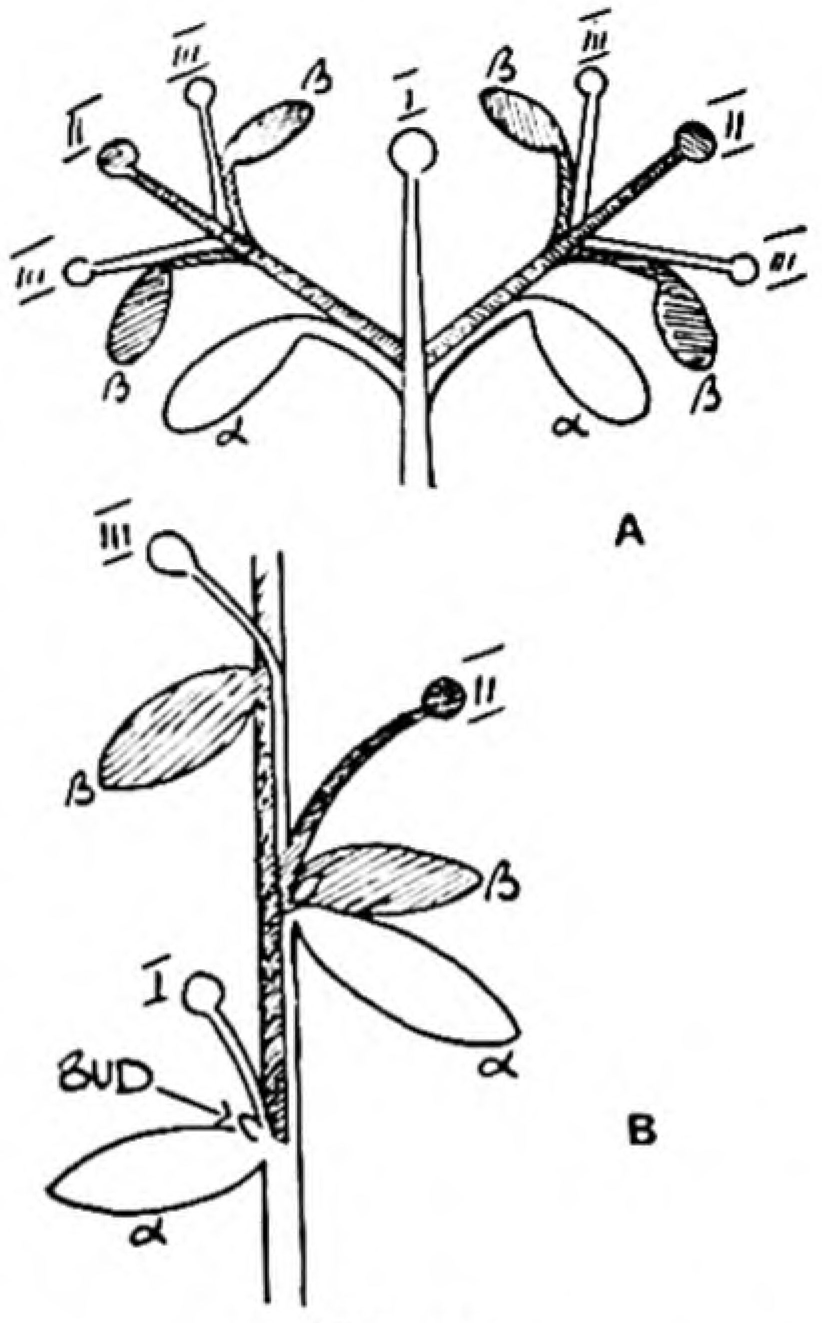


Fig. 50.

A, *Datura Stramonium*, modified dichasium.

B, *Atropa Belladonna*, dichasium reduced to a cincinnus.

In *Taraxacum*, *Elephantopus* and many primulas the plant appears to consist only of a root surmounted by a rosette of leaves. In fact, we have in these plants a root and a very short stem with extremely short internodes, and it is these two characters that give the impression of a crown of leaves borne directly on a root.

Aerial shoots may serve as water-storage organs, as in many cacti and other succulent plants (see Fig. 138). The leaves are often reduced or absent and the peripheral regions of the stem are green and carry on many of the functions normally performed by the leaf, whilst the central region of the stem consists of specialised water-storage tissue.

Aerial stems may show modifications of form associated with food storage. Parts of the swollen "root" of the radish and turnip and of celeriac are in reality stems, whilst in the kohl-rabi the whole of the swollen storage-organ is stem and bears leaves and leaf-scars.

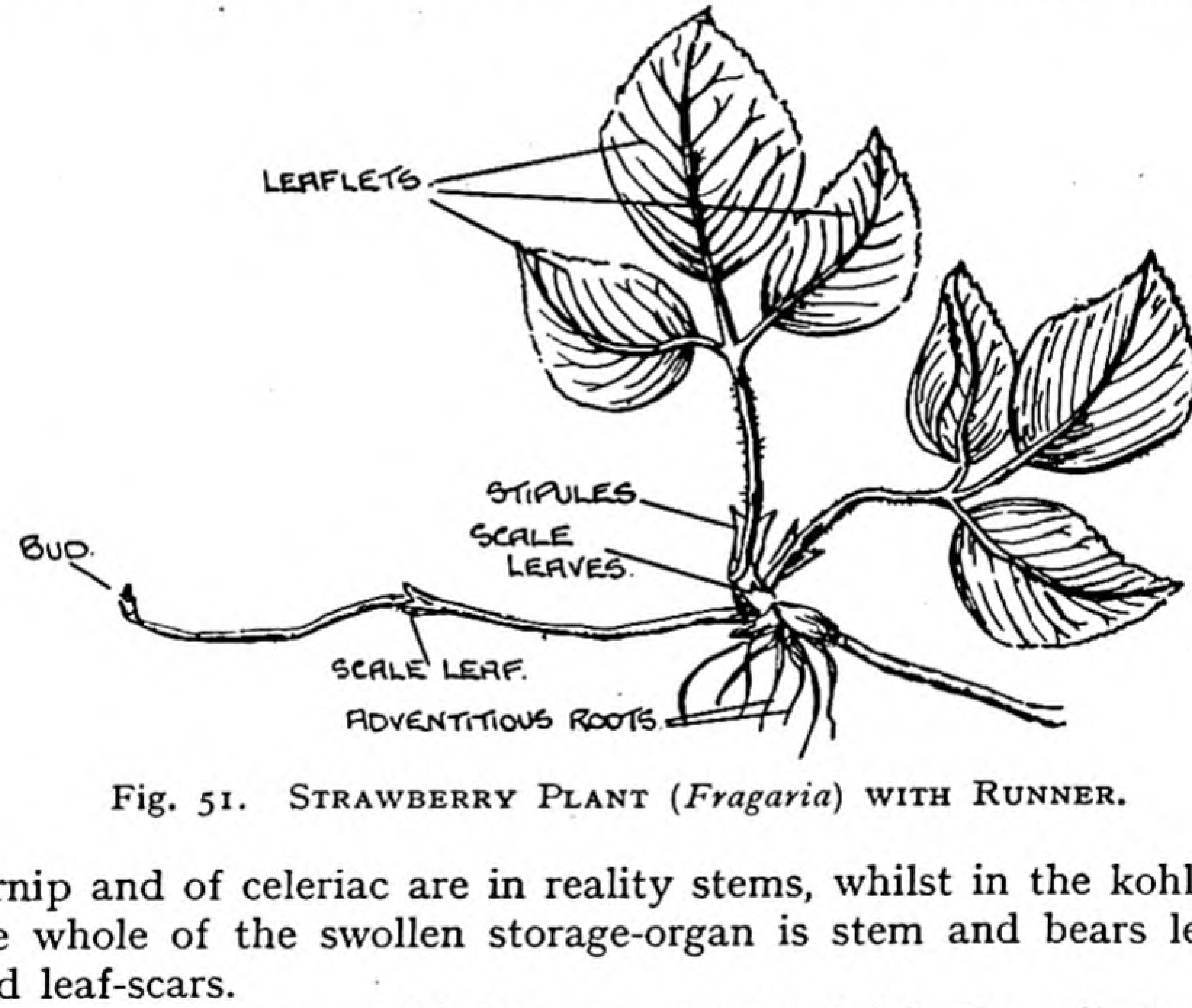


Fig. 51. STRAWBERRY PLANT (*Fragaria*) WITH RUNNER.

Most stems are aerial, but some are buried in the soil, forming underground or subterranean stems.

7. Weak Stems

In some plants the stems are more or less prostrate or trail along the ground. The weak stems of many plants, however, which are unable to grow erect, make their way upwards by attaching themselves to surrounding objects. These are **climbing** and **twining** plants.

In **climbing plants** the climbing is effected in various ways. *Ficus repens*, for example, climbs by means of adventitious roots;

these roots, developed on the stem, fix themselves to the support on which the plant climbs. *Lathyrus*, *Passiflora*, *Vitis*, and many other plants, climb by means of special organs called **tendrils.** These tendrils, as we shall see later, may be specialised stems, leaves, or parts of leaves. Virginian creeper (*Ampelopsis*) climbs by means of adhesive, sucker-like discs developed at the tips of the branches of its tendrils; *Clematis*, by means of its leaf-stalks or petioles, which act as tendrils, and, in fact, are called *petiole tendrils*. In some plants, e.g. *Artabotrys*, *Unona* and *Strychnos*, a modified inflorescence-axis forms a sensitive hook, which, after attaching itself to a support, thickens and becomes woody. The leaf-tip of *Gloriosa* is sensitive and functions as a tendril.

As distinguished from these, **twining plants** achieve the same result by twining round some support, as for example, *Convolvulus*, *Thunbergia*, *Ipomoea*, and *Phaseolus* (see Fig. 166). Climbing in all cases enables plants with weak stems to attain such a position that their foliage leaves can receive adequate illumination and so be enabled to carry on the process of photosynthesis.

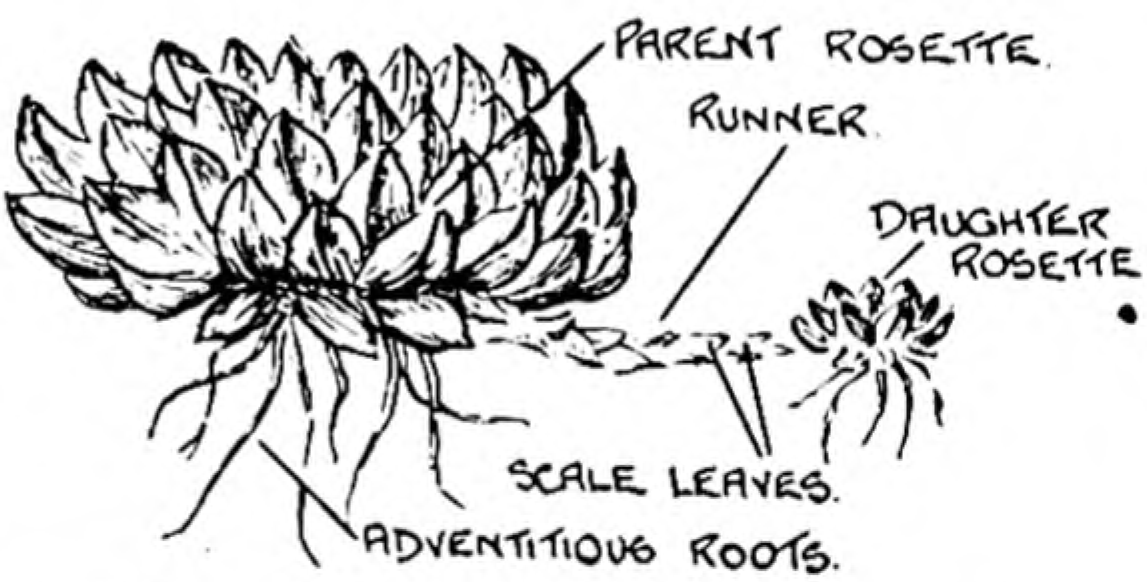


Fig. 52. *Sempervivum* WITH OFFSET.

8. Runner, Offset, and Sucker

Many plants give off highly specialised shoots, serving chiefly for purposes of vegetative reproduction. Of these the runner, offset, and sucker are the commonest.

The **runner,** or *stolon* (Fig. 51), is a slender shoot running along the surface of the ground, and attaining a considerable length. It arises in the axil of a leaf, at the level of the soil. At intervals it produces small scale-leaves, with a bud in the axil of each. From the bases of these buds adventitious roots pass down into the soil, and in this way new plants are formed. Strawberry, *Launea pinnatifida*, *Ipomoea Pes-caprae* and *Nephrolepis* give good examples. An advantage of this habit of growth is that it enables a single plant to cover a large area of ground with great rapidity. In plants like the blackberry (*Rubus*) the tips of the ordinary vegetative stems, after scrambling over a support may come to rest on the soil, where they take root and a new plant arises.

The **offset** resembles the runner in origin, but is shorter and stouter. It is a short runner which turns up at the end to form a new plant, and occurs in *Agave* and house-leek (*Sempervivum*, Fig. 52).

The **sucker** (Fig. 53) is an *underground* runner or branch which grows upwards, and develops roots and aerial shoots. The sucker may be a branch arising from an axillary bud on an underground stem, e.g. mint and dead-nettle. It may also arise from an adventitious bud on a root, as in plum and rose. Underground suckers have a root-like appearance but they can be distinguished as stems by the possession of scale-leaves, and often by their mode of origin.

9. Bulbils

These may be described as axillary buds, which become large and fleshy owing to the storage of food-material in their leaves. They differ also from ordinary buds in the fact that they separate from the parent plant, fall to the ground, and produce new plants, thus serving for reproduction (e.g. *Remusatia*, some lilies). They may also take the place of flowers (e.g. in onion, *Globba*, *Agave*, some grasses, etc.). In those plants which produce them seed-formation is usually very uncertain.

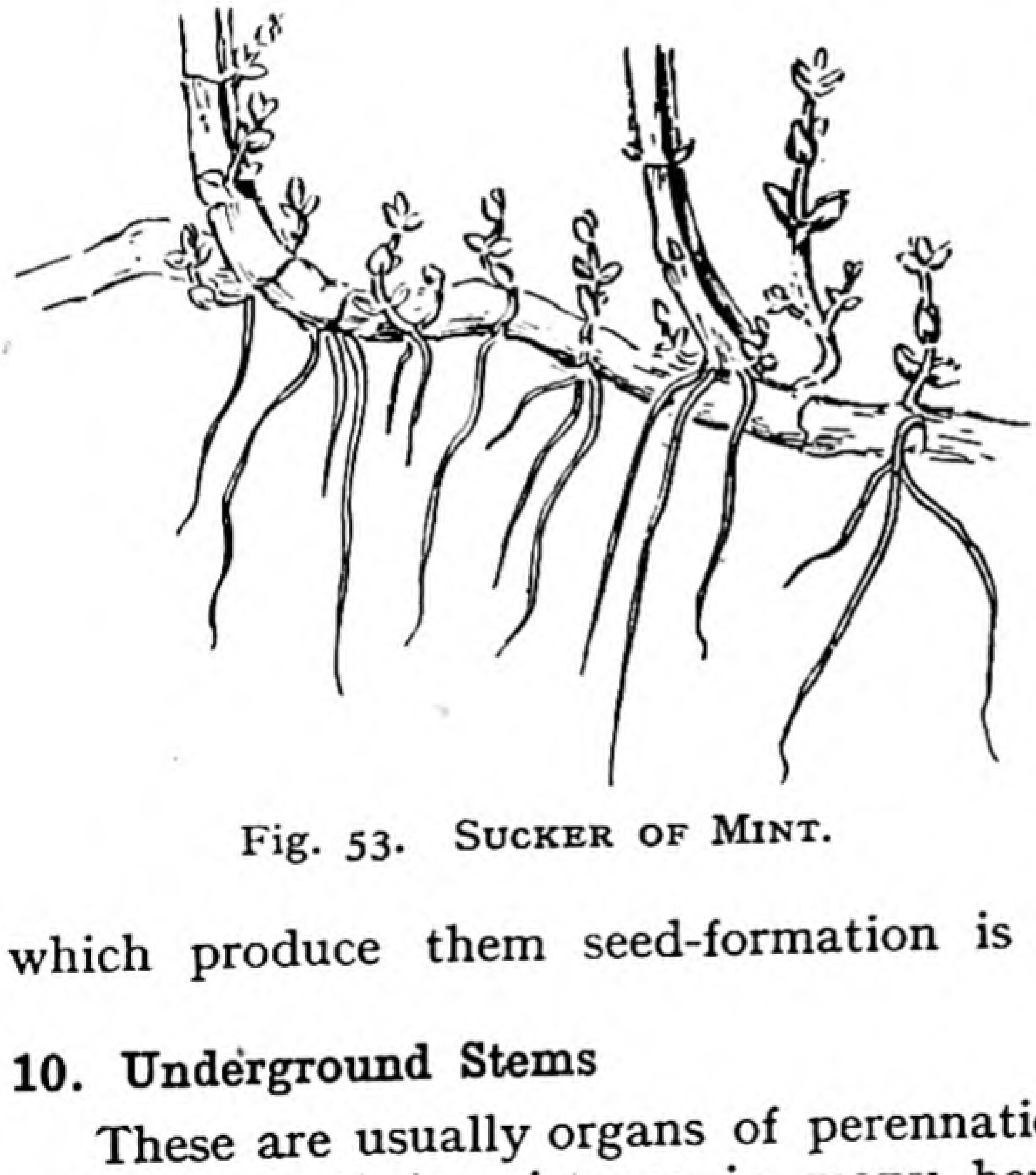


Fig. 53. SUCKER OF MINT.

10. Underground Stems

These are usually organs of perennation, and we have already pointed out their existence in many herbaceous perennials. As with some surface creeping stems they serve as organs of vegetative propagation and sometimes enable plants rapidly to colonise large areas of ground.

Rhizomes are underground stems which grow more or less horizontally beneath the surface of the soil. They may be superficially root-like, but they can be distinguished from roots by the presence of leaves and buds. The leaves may be large foliage leaves which come above ground, or, more frequently, the rhizome bears scale-leaves which may be very much reduced. Aerial shoots develop from buds in the axils of these scale-leaves, or from terminal buds, whilst numerous adventitious roots develop a fibrous root-system. Rhizomes are frequently thick and fleshy and serve as storage organs (e.g. *Dioscorea villosa* and *D. quinqueloba*). The rhizome of *Iris* bears foliage leaves and flowers from the turned-up ends of its branches, whilst on the older portion scars mark the position of earlier leaves. Further growth of the rhizome takes place from one or more buds, usually formed in the axils of leaves at the base of the aerial shoot. Other examples are seen in the Zingiberaceae, e.g. *Zingiber*, *Elettaria*, *Curcuma*, *Amomum*.

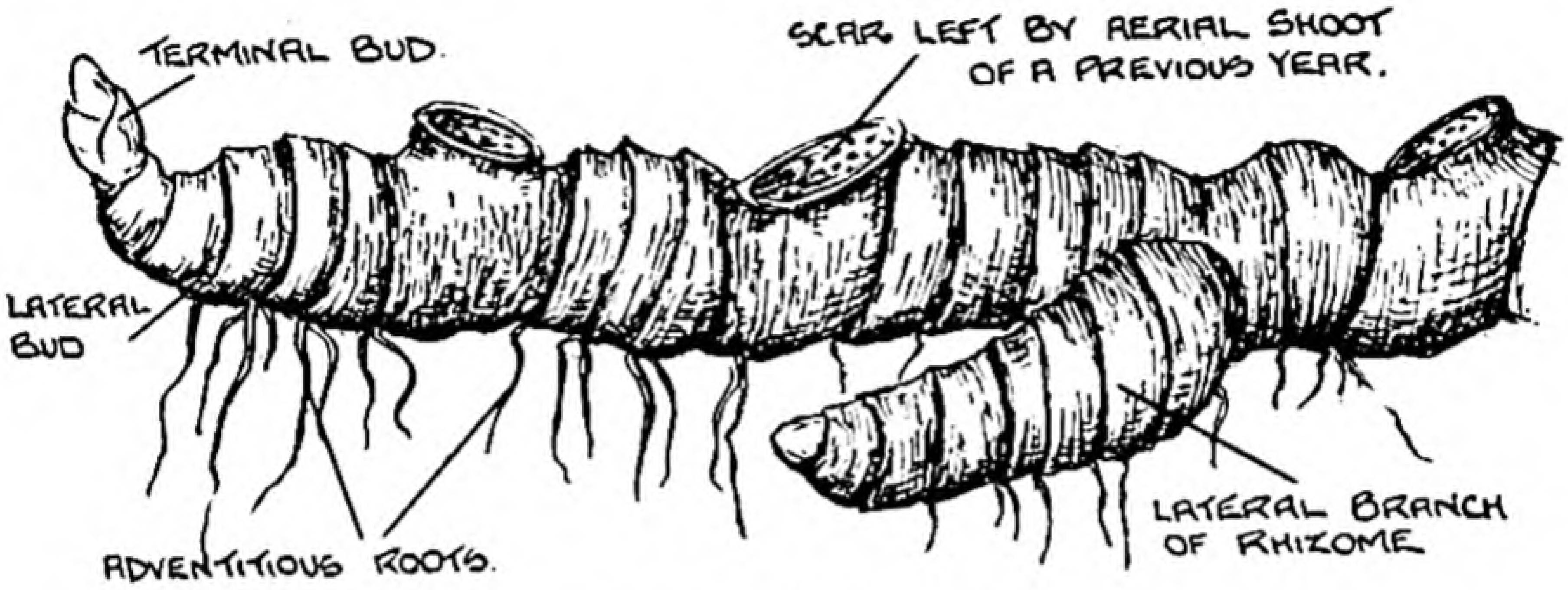

TERMINAL BUD.
SCAR LEFT BY AERIAL SHOOT OF A PREVIOUS YEAR.
LATERAL BUD
ADVENTITIOUS ROOTS.
LATERAL BRANCH OF RHIZOME

Fig. 54. SOLOMON'S SEAL RHIZOME.

In *Polygonatum*, (Fig. 54) also the aerial shoots are produced from buds which terminate the branches of the rhizome. At the end of each growing season, each aerial shoot dies down, leaving a circular scar. The length of rhizome between two such scars represents one year's growth, and is covered by numerous leaf scars encircling it. A number of axillary buds may be produced, but one near the base of the aerial shoot enlarges to become next year's continuation of the rhizome, and other buds may give rise to branches. These may be separated for vegetative propagation and, in Nature, do become separated as they grow and the older parts of the rhizome decay. *Iris* and Solomon's seal show sympodial growth in their massive, fleshy stems. Examples of slender sympodial rhizomes are found in sedges (Fig. 55), grasses, e.g. couch-grass (*Agropyron*) etc. The aerial branches may be given off in a racemose manner, in which

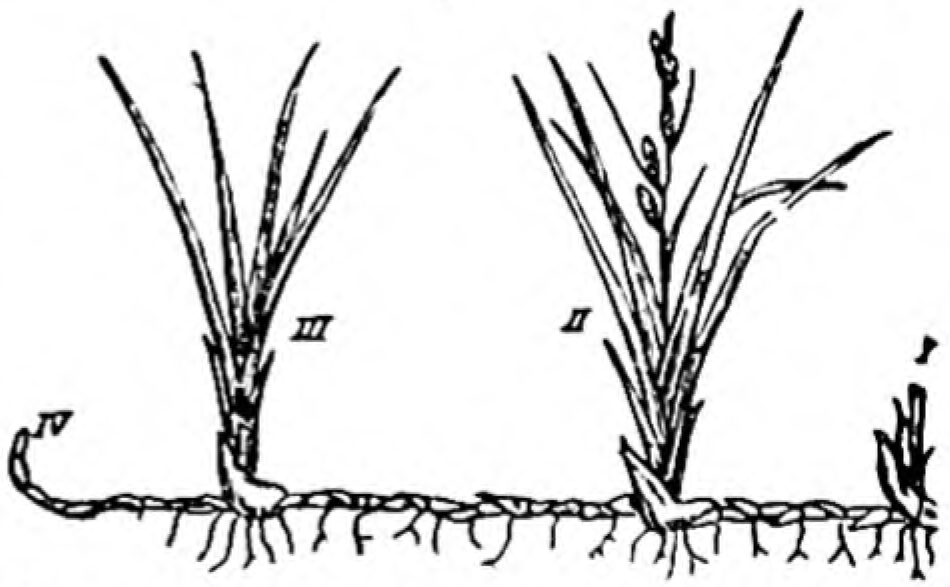


Fig. 55. RHIZOME OF SEDGE (CAREX) IN SUMMER.

Flowering shoots of (I) last year, (II) this year, (III) next year, (IV) year next but one.

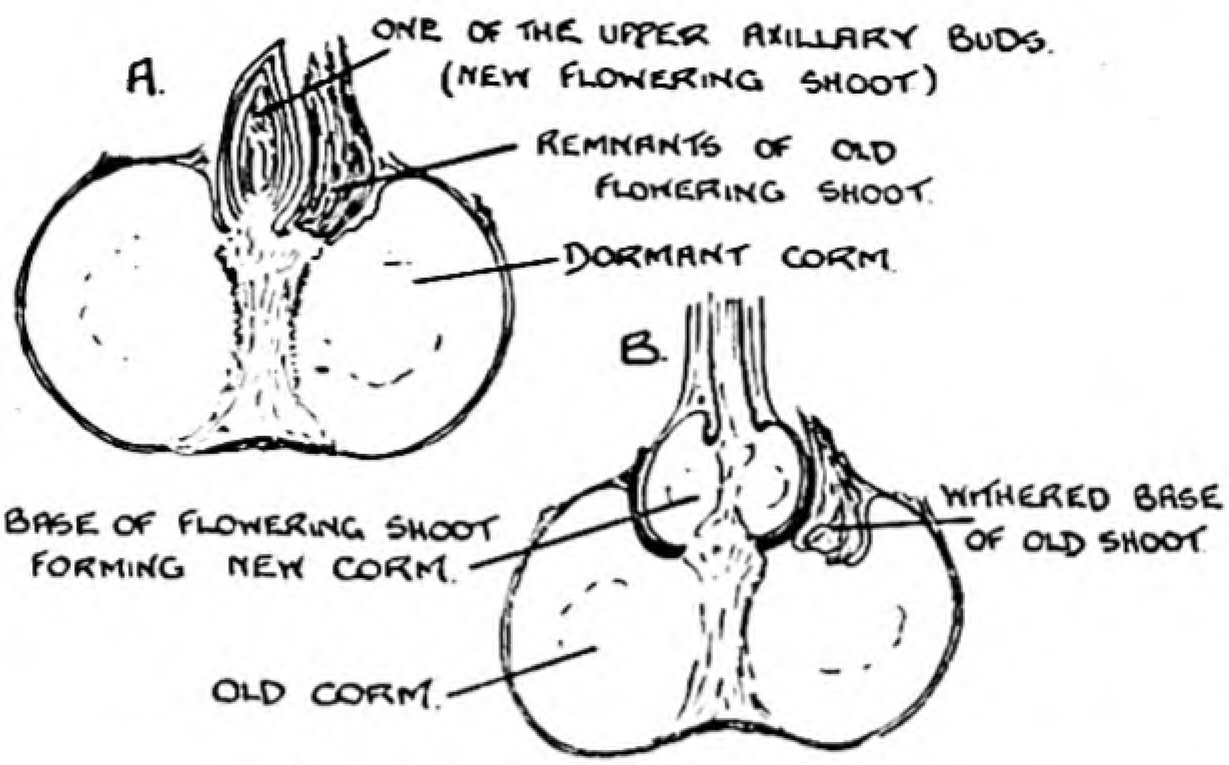

A.
ONE OF THE UPPER AXILLARY BUDS. (NEW FLOWERING SHOOT)
REMNANTS OF OLD FLOWERING SHOOT
DORMANT CORM
B.
BASE OF FLOWERING SHOOT FORMING NEW CORM.
WITHERED BASE OF OLD SHOOT
OLD CORM.

Fig. 56. *Crocus* CORM, L.S.
A, Dormant ; B, At time of flowering.

case the rhizome is monopodial in development and has a persistent apex (e.g. *Oxalis*). Root-stocks are really short rhizomes which are more or less erect. Examples occur in various primulas, *Rheum*, etc.

The **Corm** (Figs. 56 and 57) is a condensed form of rhizome or root-stock. It consists of a solid swollen stem, on which are a number of loose, more or less sheathing scale-leaves. The size of the stem is due to the large amount of food-material stored in it. One or more buds are present in the axils of the leaves, sometimes towards the apex of the stem (e.g. in crocus, Fig. 56), sometimes towards the base (e.g. in autumn crocus or meadow saffron, Fig. 57). These buds are already provided with leaves whose bases ensheath an erect, shortened stem. The stem apex terminates in a flower. In the spring the buds develop at the expense of the stored food-material in the corm and grow up into aerial shoots. Adventitious roots are developed from the base of the shoot, and pass down into the soil. During the summer the surplus amount of substance manufactured by the leaves is stored up in the stem of the new shoot, and thus a new corm is gradually formed. This remains covered by the dried, membranous bases of the leaves of the aerial shoot as it dies down. The corm thus formed rests in the ground with certain of its lateral buds enlarged and protected by the membranous leaf bases. The growth of the corm is therefore sympodial.

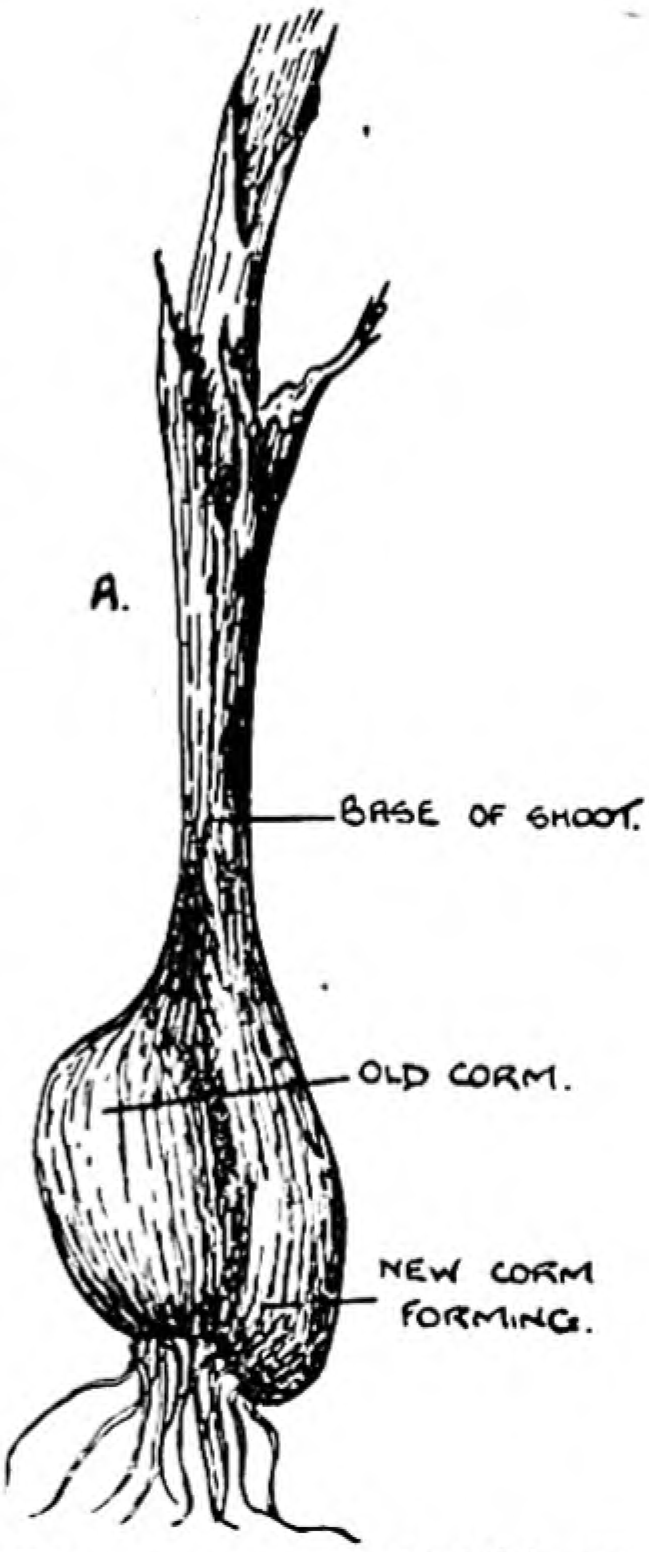

A.
BASE OF SHOOT.
OLD CORM.
NEW CORM FORMING.

Fig. 57, A. *Colchicum autumnale.*
Base of Plant, External.

Corms also occur in *Iphigenia, Montbretia, Gladiolus, Cyclamen* and *Testudinaria*. In the latter two plants the corm is not renewed annually as it is in *Crocus*, but is a perennial structure.

The **Bulb** (Fig. 58) may also be regarded as a short specialised underground shoot. The stem, however, remains comparatively small, and the food-material is stored in the large, fleshy scales which invest and overlap the stem. These scales may either be scale-leaves, or the fleshy bases of foliage leaves whose upper parts have withered. Buds are present in the axils of the scales, and in the spring one or more develop at the expense of the stored food-material into a flowering axis surrounded by foliage leaves, and also, it may be, by a number of scale-leaves. Adventitious roots grow from the base of the bulb.

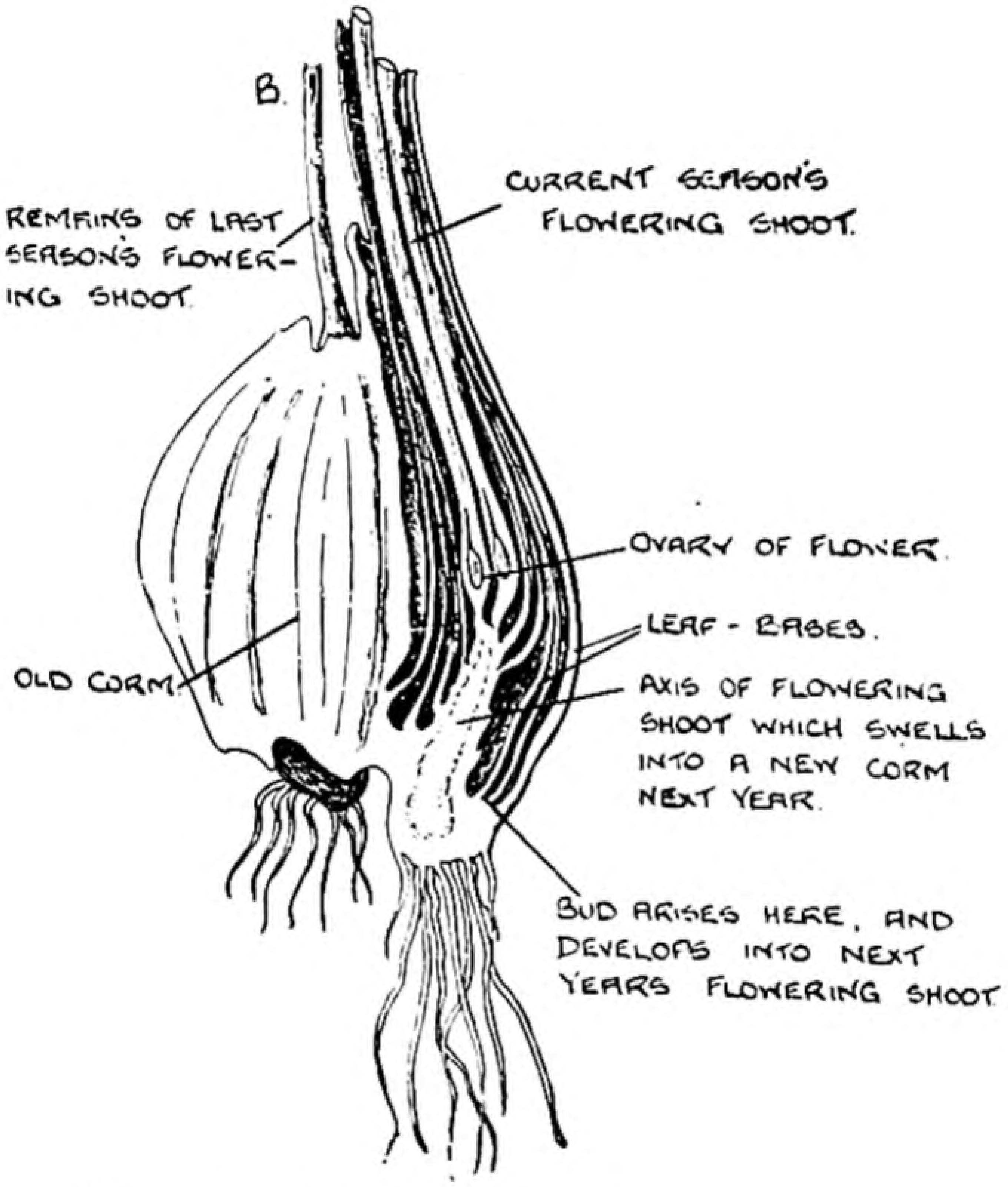

B.
REMAINS OF LAST SEASON'S FLOWERING SHOOT
CURRENT SEASON'S FLOWERING SHOOT.
OVARY OF FLOWER.
LEAF - BASES.
OLD CORM
AXIS OF FLOWERING SHOOT WHICH SWELLS INTO A NEW CORM NEXT YEAR.
BUD ARISES HERE, AND DEVELOPS INTO NEXT YEARS FLOWERING SHOOT

Fig. 57, B. L.S. Corm of *Colchicum autumnale*.

The surplus food-material which is formed by the foliage leaves is stored either in their bases or in the scale-leaves of one or more of the axillary buds, and in this way new bulbs are produced which will repeat the process the following year.

In **scaly bulbs** (e.g. *Lilium, Urginea*), the fleshy scales composing the main bulk of the bulb overlap at their margins. In **tunicated bulbs** (e.g. *Allium*, tulip, and hyacinth) the outer leaves are large and completely ensheath the inner portions of the bulb. The coloured membranous covering present on the outside of such bulbs is formed by the shrivelled remains of either leaves of a previous season, or by an outer membranous scale-leaf.

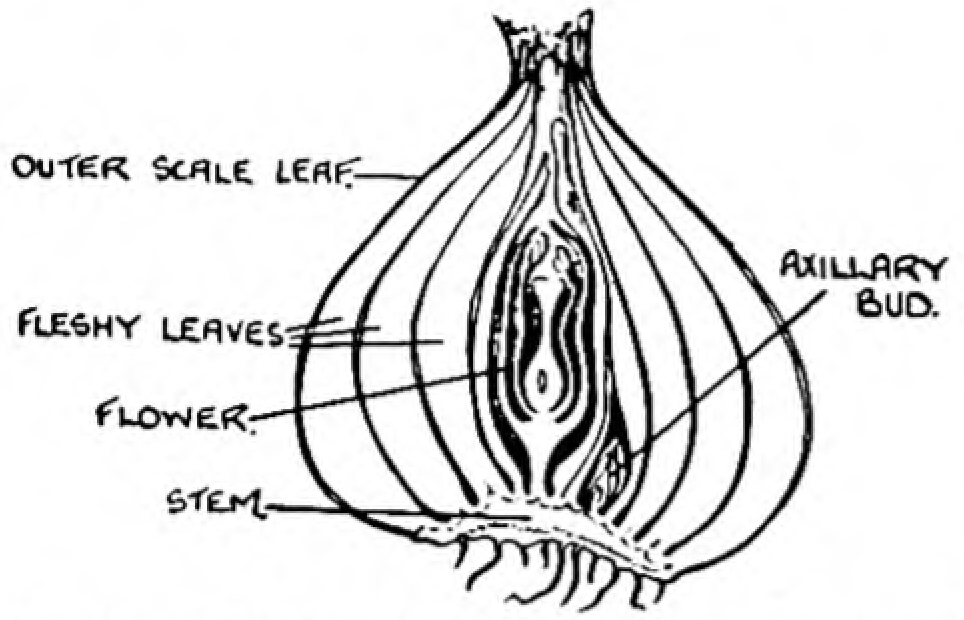


Fig. 58. *Tulipa*: BULB IN LONGITUDINAL SECTION.

Bulbs and corms are organs of perennation and of vegetative propagation. Whilst still underground, the organs of the aerial shoot, including the parts of the flower, are already formed in their buds. Hence they develop quickly as soon as suitable conditions prevail—usually in the spring. Their offspring multiply rapidly, though they do not spread as rapidly as rhizomes, but tend to remain in close proximity to the parent plant. Some bulbous plants, e.g. bluebells, cover large tracts of woodland, but these colonies indicate a long period of undisturbed development, and also considerable propagation by seed.

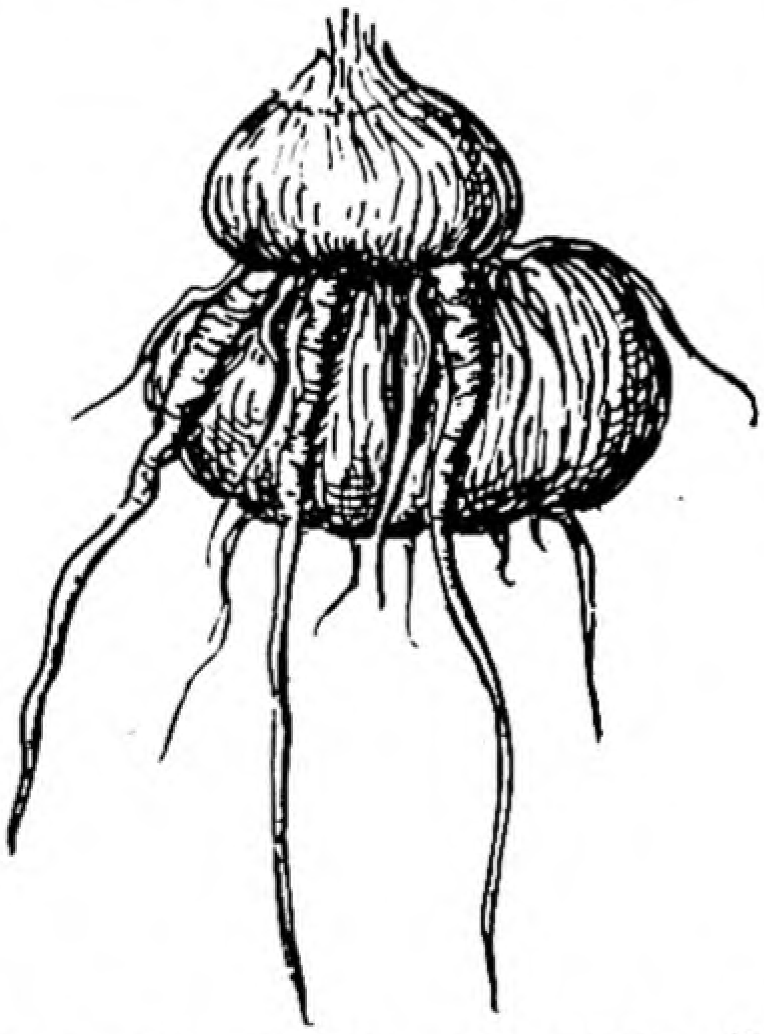


Fig. 59. CORM SHOWING CONTRACTILE ROOTS.

The depth below soil level at which a bulb, corm or rhizome grows is fairly constant for a given species, but owing to their manner of growth there is a tendency for each successive generation to be raised above the preceding one. In order to compensate for this, contractile roots are developed in some plants. These contractile roots, because of their peculiar properties, are able to pull down the bulb or corm to its required depth in the soil (Fig. 59). More or less constant depth may also be maintained as the result of raising of the soil level by the large quantity of humus formed.

The **Stem-tuber** is a swollen underground stem or part of a stem, which serves both as an organ of vegetative reproduction and as a storage organ. In the potato plant (*Solanum tuberosum*) slender stolons or rhizomes arise from the buds in the axils of the basal leaves of the shoot. The ends of these, and of their lateral branches, swell to form the potatoes. The potato tuber can readily be identified as a stem structure because of the presence of buds—a terminal one at or near one end, and lateral ones in the axils of very much reduced leaves (the " eyes ") arranged spirally round the stem-tuber (Fig. 60). There is a scar at the other end. The tuber contains starch and some protein, and the brown covering consists of a thin layer of cork tissue. Thus the potato tuber represents several internodes of the underground stem. The tuber of Jerusalem artichoke (*Helianthus tuberosus*) is similar but the lateral buds occupy projections on the surface of the tuber, and the stored food-material consists mainly of inulin. In Chinese artichoke (*Stachys tubifera*) the tuber is formed of a series of swollen internodes, in which, as a food reserve, is stored stachyose, a carbohydrate, each molecule of which consists of one fructose, one glucose and two galactose units.

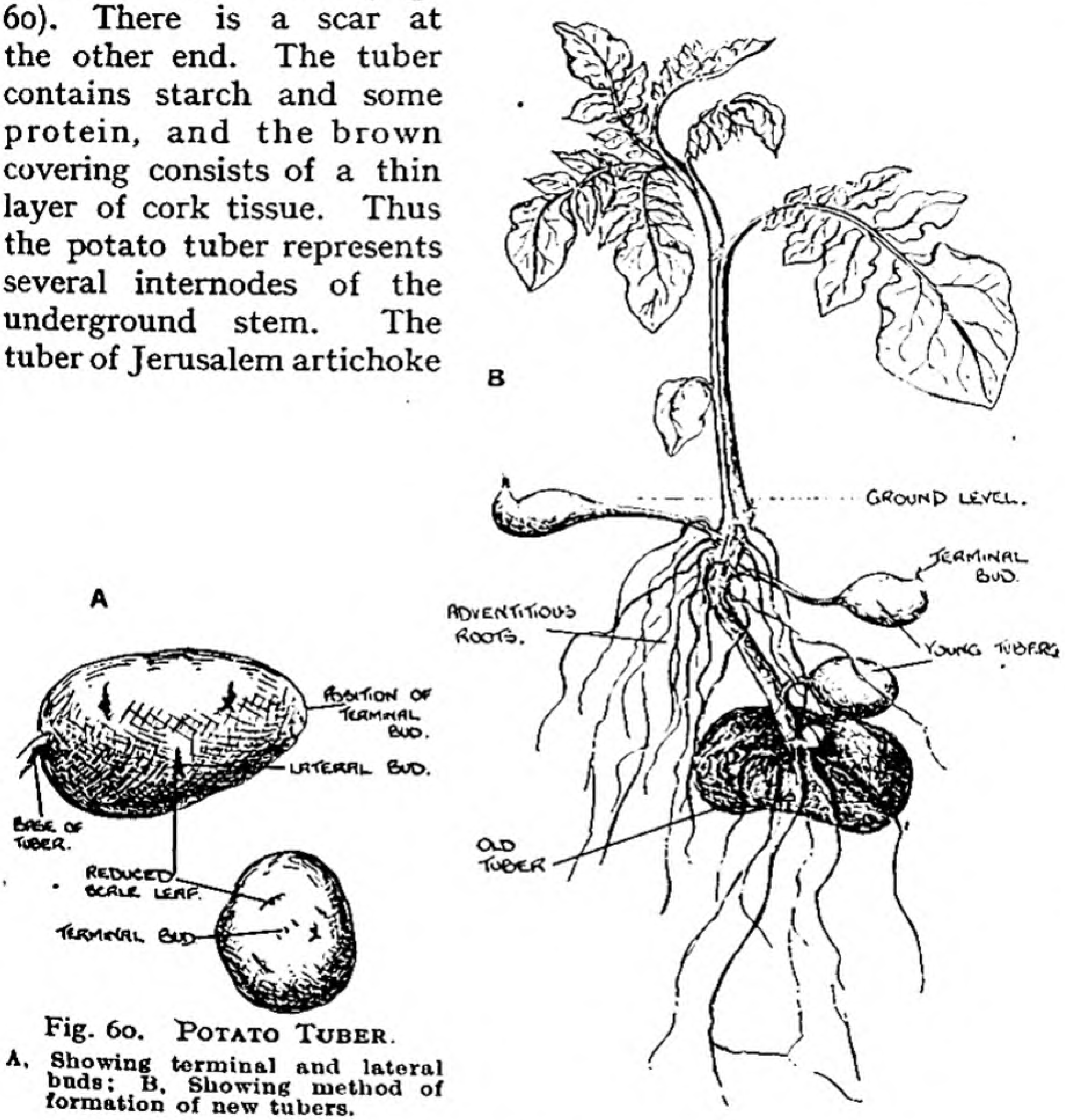

B
GROUND LEVEL.
TERMINAL BUD.
ADVENTITIOUS ROOTS.
YOUNG TUBERS
OLD TUBER
A
POSITION OF TERMINAL BUD.
LATERAL BUD.
BASE OF TUBER.
REDUCED SCALE LEAF.
TERMINAL BUD.

Fig. 60. POTATO TUBER.
A, Showing terminal and lateral buds; B, Showing method of formation of new tubers.

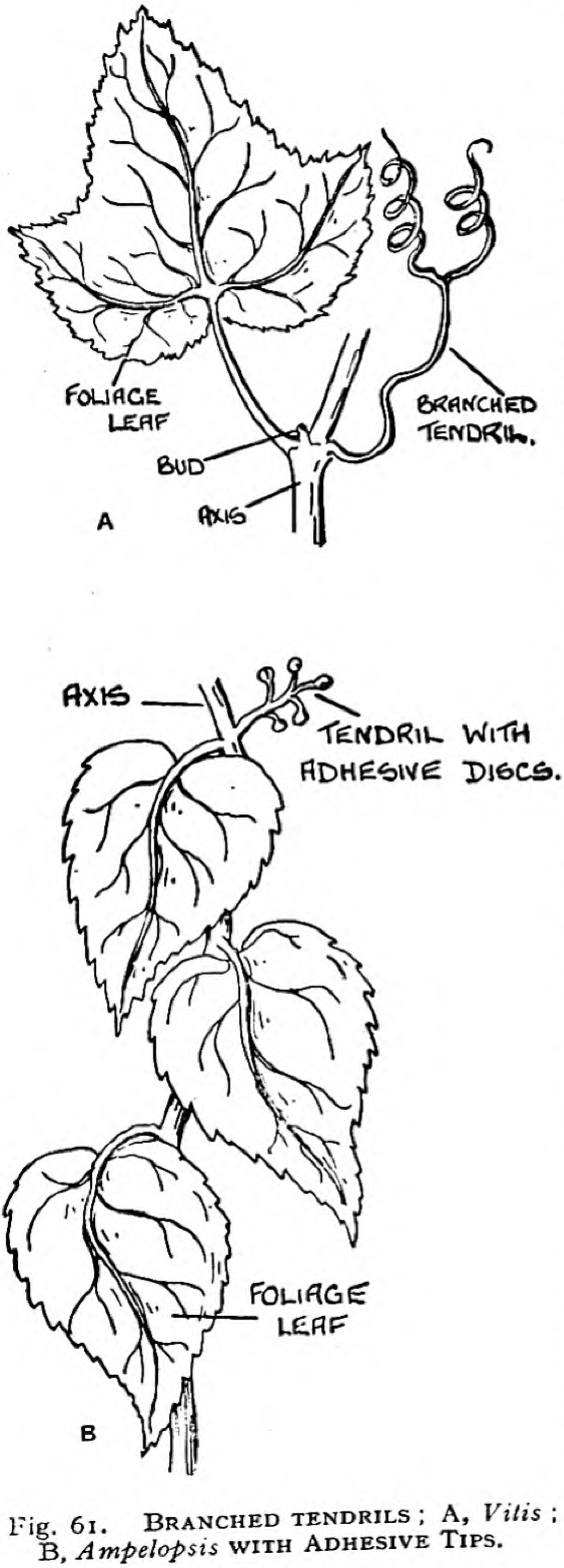


Fig. 61. BRANCHED TENDRILS; A, *Vitis*; B, *Ampelopsis* WITH ADHESIVE TIPS.

11. Stem-tendrils, Spines, and Cladodes

These are striking examples of pronounced modification of form and function exhibited by some stems. They are externally quite unlike ordinary stems, but their stem nature can be distinguished by their mode and place of origin and development.

STEM-TENDRILS (Fig. 61, also Fig. 167).—These are highly specialised climbing organs. They are slender, often branched and may bear small scale-leaves. When still elongating the apical part of a tendril exhibits regular movement, and if in the course of this movement it comes into contact with a slender, solid object, the tendril coils around it. The young tendril is sensitive to contact, but it loses this sensitivity with age. When the apical part of the tendril has coiled around the support, that part between the support and the plant becomes spirally coiled, but forms two spirals in opposite directions separated by a point of reversal. Thus the plant is fixed to the support by a strong but elastic connexion.

The tendril may represent an axillary shoot, e.g. *Passiflora*. The tendrils of

Vitis (vine) and *Ampelopsis* (Virginian creeper), Fig. 61, are variously interpreted, e.g. as the modified growing-points of the successive axes of a sympodium, or, as derived from leaf-primordia of a monopodium.

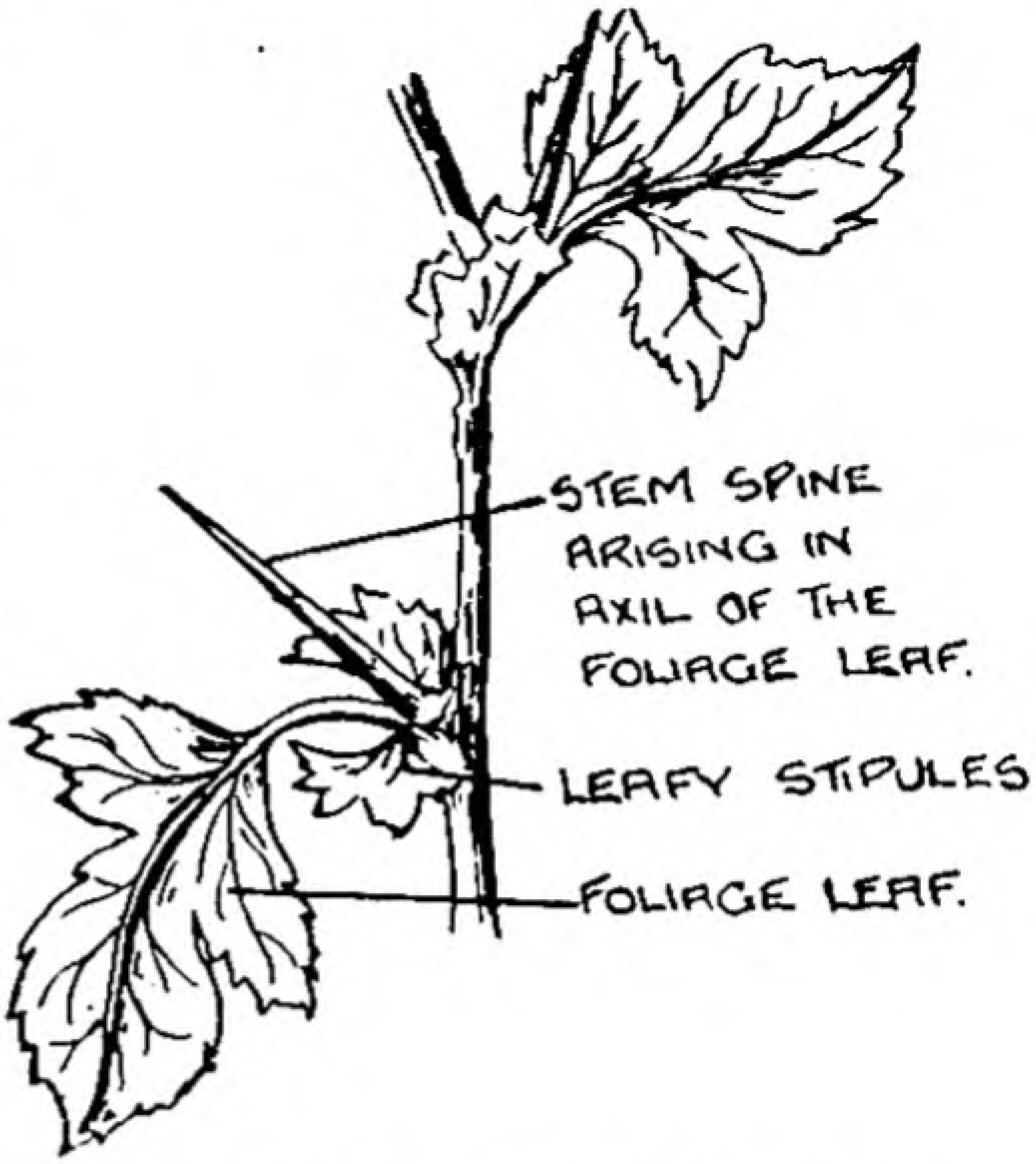


Fig. 62. *Crataegus*, STEM-SPINE.

STEM-SPINES, OR THORNS.—These are modified branches which have lost their apical growing point and become hard and sharp-pointed. Examples are seen in *Carissa, Colletia, Crataegus* (Fig. 62) and *Ulex* (Fig. 112, c). Stem-spines may be recognised as stems by their position in the axils of leaves, and by the fact that they may bear scale-leaves and lateral buds. They may develop as a response to dry conditions and their formation in the gorse can be suppressed by growing the plant in a very humid atmosphere. But in most spinous plants the spines develop no matter what the conditions under which the plant is grown.

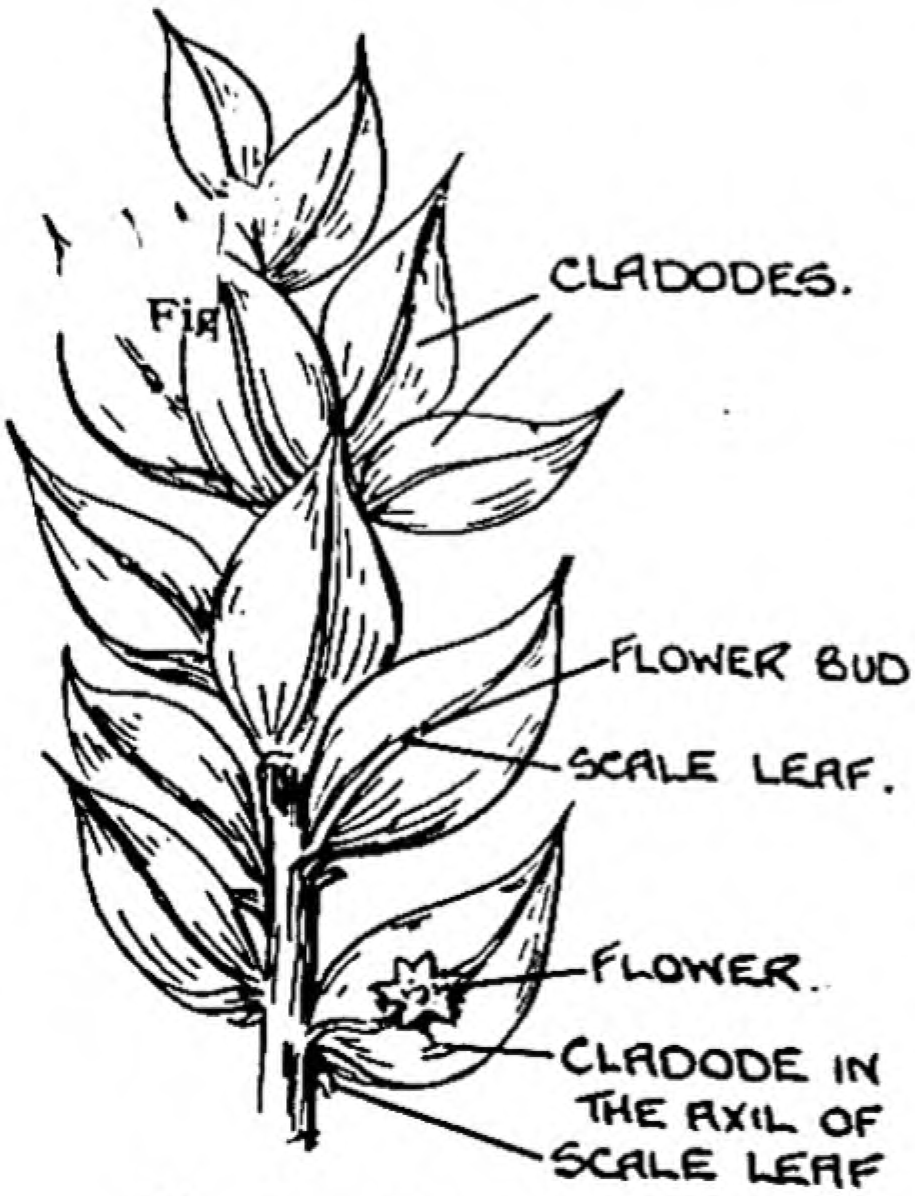


Fig. 63. *Ruscus*, CLADODES.

CLADODE OR PHYLLOCLADE.—This is a stem-structure which has taken on the general appearance and functions of a leaf. The whole stem may be so modified. This is the case, for example, in duckweed, a small aquatic Monocotyledon in which the minute leaf-like stem not only carries on the process of photosynthesis, but also acts as a float. Usually, however, phylloclades represent lateral branches. In *Ruscus aculeatus*, butcher's broom (Fig. 63), they are leaf-like externally, but bear flower-buds and arise in the axils of small scale-leaves. Species of *Phyllanthus* have flat, green phylloclades bearing flowers on the margins. Asparagus has green needle-like phylloclades.

The flat stems of many cacti and other succulent plants (e.g. *Euphorbia*, Fig. 138) are to be regarded as phylloclades also. When phylloclades are present, the true leaves are generally reduced to small, often brown, scales, or they may be very short-lived, falling off at an early age, leaving all the normal leaf functions to be carried on by the phylloclades.

12. Summary

We may summarise the general distinctive characters of the stem in the following statement: stem-structures *tend* to grow *upwards, towards the light*; they usually end in a bud, and bear leaves, lateral buds, and often also reproductive organs; lateral branches (in Spermatophyta) arise in the axils of leaves; their development and internal structure are, in many ways, characteristic.

We cannot, however, regard this as of the nature of a definition, distinctly marking off stems from leaves and roots, for these general characters are not absolute. Thus we have seen that some stems (e.g. rhizomes) remain underground and partake of the functions of roots; others have lost their terminal bud; in a few cases, again, buds are developed on roots and leaves. At the same time the student must notice these characters carefully; for it is by attention to these that he can as a rule recognise members which, however modified they may be, have the morphological value of stems. In this way, as already indicated, the rhizome, the sucker, the tubers of the potato, and the spines of the sloe [illegible] be recognised as stem-structures.

B. INTERNAL STRUCTUR

I.—THE DICOTYLEDON

13. Primary Structure

A useful dicotyledonous stem in which to study the primary arrangement of the tissues is that of sunflower (*Helianthus annuus*). An internode must be chosen in which differentiation of the tissues derived from the apical meristem is more or less complete, but in which little or no secondary growth has taken place. A relatively small number of internodes a short distance below the apex show this condition. If the stem of the Jerusalem artichoke (*Helianthus tuberosus*) is available, it affords a larger number of internodes in this condition, and is similar in structure (Fig. 64).

If we cut an internode transversely, and examine the cut surface with a hand lens we shall see, a short distance from the exterior, a ring of separate vascular bundles, surrounding a relatively wide pith. For further details we must proceed to study a thin transverse section under the microscope. For this purpose a sharp razor is necessary, and sections so obtained must be treated in various ways. For preliminary examination it is useful to stain a section with iodine solution in potassium iodide, and mount it on a slide under a coverslip in dilute glycerin. The iodine stains the starch grains blue-black, protoplasm pale yellow, nuclei deeper yellow and lignified cell-walls yellow-brown. It serves, therefore, as a good differential stain.

On the outside is the **epidermis**, consisting of regular, rectangular cells, their outer walls cuticularised. Here and there multicellular trichomes arise from it and stomata are present. Within this is the **cortex**, a narrow zone consisting of living cells. The ones below the epidermis are **collenchyma.** These gradually merge into **parenchyma**, that is, the thickening at the angles becomes less in amount as we pass from the outer to the inner cells of the cortex, and the intercellular spaces become larger and well defined. Chloroplasts are present in both types of cell, and transitory starch is formed as a result of photosynthesis. The innermost layer of the cortex is the **endodermis**, or **starch-sheath**, which consists of one layer of cells, each containing a number of small, permanent starch-grains, which render it readily identifiable in iodine-stained preparations, where it stands out as a wavy line just outside the

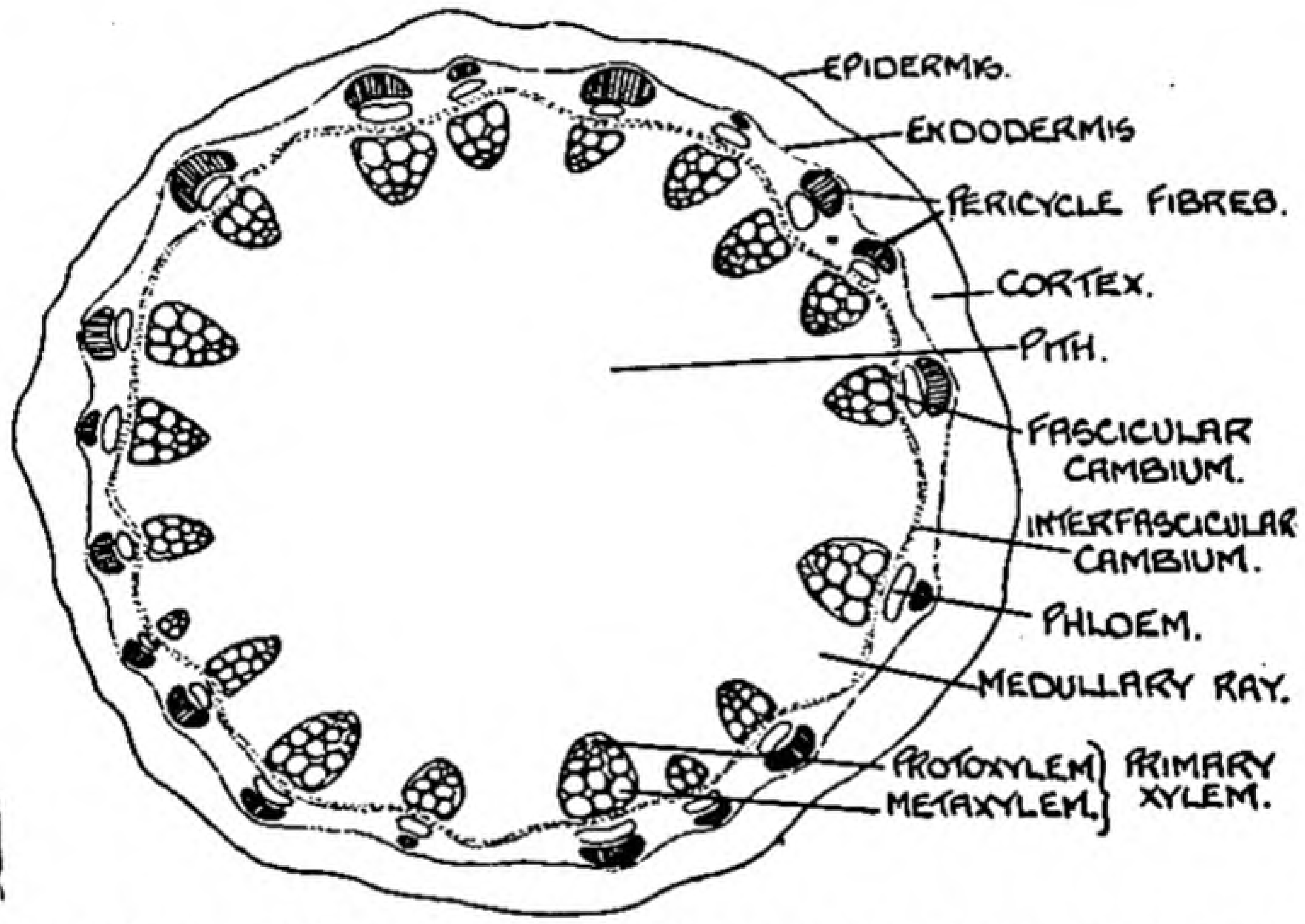


Fig. 64, A. *Helianthus*, STEM: TRANSVERSE SECTION, DIAGRAM.

ring of vascular bundles. Here and there, in the cortex may be seen schizogenous oil ducts each surrounded by a few epithelial cells.

All inside the endodermis is the central cylinder or stele. It consists of **pericycle, vascular bundles** separated by **medullary rays** and **pith**.

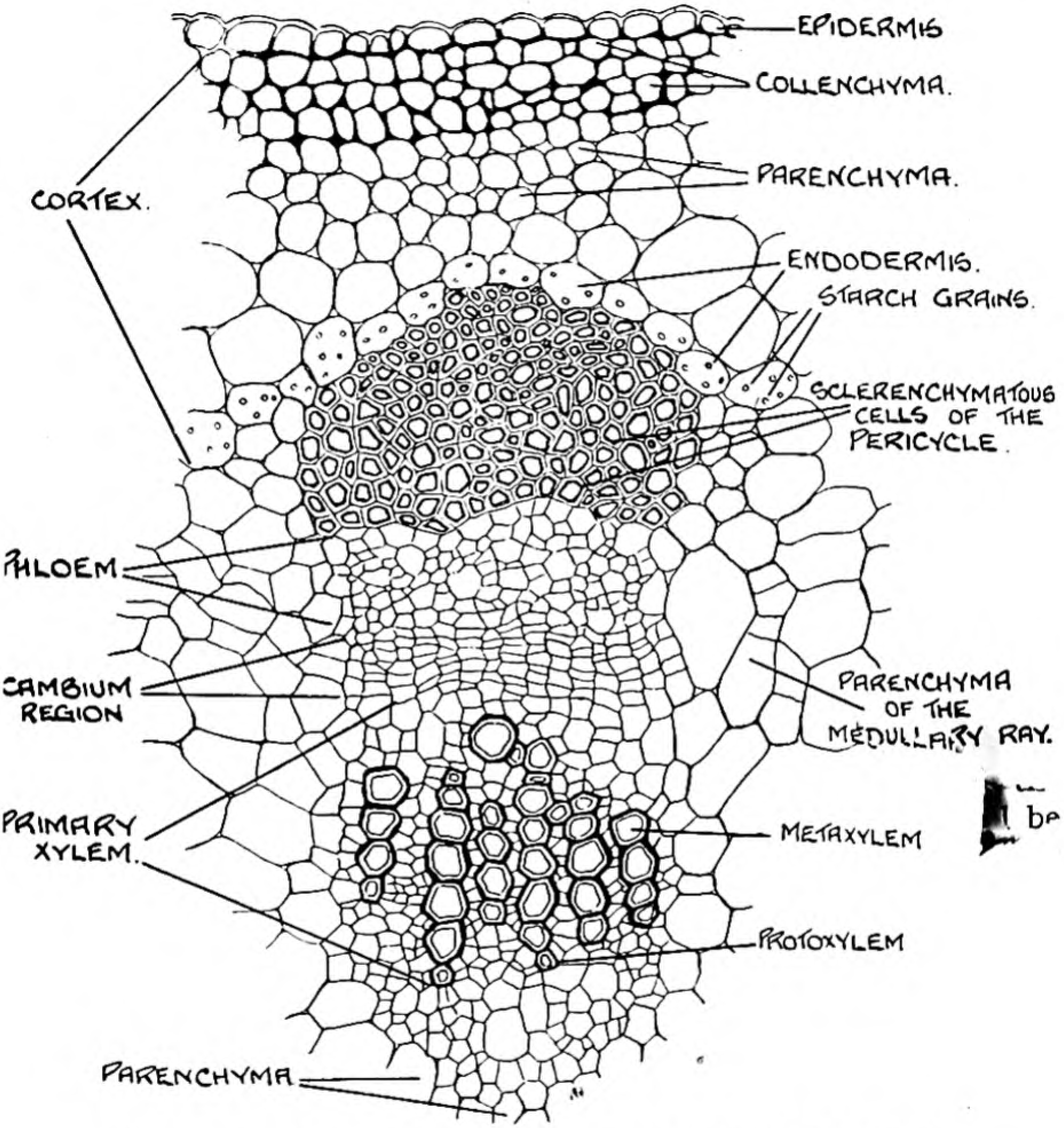

EPIDERMIS
COLLENCHYMA.
PARENCHYMA.
CORTEX.
ENDODERMIS.
STARCH GRAINS.
SCLERENCHYMATOUS CELLS OF THE PERICYCLE.
PHLOEM
CAMBIUM REGION
PARENCHYMA OF THE MEDULLARY RAY.
PRIMARY XYLEM.
METAXYLEM
PROTOXYLEM
PARENCHYMA

Fig. 64, B. Detailed drawing of portion of Fig. 64, A.

The **pericycle** is most obvious immediately outside each vascular bundle, where it occurs as a bundle of sclerenchymatous fibres. When fully mature these are thick-walled and lignified. Within the pericycle is the **phloem**, consisting of **sieve-tubes, companion cells** and **phloem parenchyma**. The companion cells are small but have a nucleus and are filled with dense contents which stain deeply with iodine solution. The sieve-tubes are larger, and may appear empty, except where the section has cut through a **sieve-plate.** These traverse the sieve-tubes at intervals and show the characteristic perforations. The rest of the sieve-tube has a thin lining of cytoplasm within the cell-wall enclosing a vacuole filled with elaborated food-material. Within the phloem is a narrow zone of **conjunctive parenchyma**, thin-walled cells associated with the **cambium.** The cambium is meristematic. The inner portion of the vascular bundle is made up of **xylem.** This primary xylem is differentiated into an outer **metaxylem** of **pitted vessels** and **tracheides,** dead elements whose walls are lignified and stain with iodine solution, and an inner **protoxylem,** consisting of **spiral** and **annular vessels,** in which the thickening bands are lignified, and also **xylem parenchyma** which are living and have cellulose walls. These cells are smaller than the parenchyma of the medullary rays and pith. They all may contain storage starch. Bundles of the type we have described are called **collateral bundles** in that they possess an inner xylem and an outer phloem on the same radius, and **open bundles** in that they possess a cambium.

We have seen (pp. 35 and 49) that such bundles are the result of the differentiation of cells which arise from the apical meristem, first appearing as desmogen strands. Within these strands the order of differentiation is from the two extremities, inwards towards the middle of the bundle. This order of differentiation can be followed when we cut serial transverse sections from the apex, backwards. The first-formed xylem is the protoxylem, and the first elements of the protoxylem to take shape are annular or spiral vessels. Both these types of vessel are laid down whilst other cells around them are still growing, *i.e.* elongating by vacuolation, or even dividing. The advantages of the annular and spiral thickening will at once be apparent, for, since these cells are dead, they cannot grow, but their walls are elastic and can be stretched as the result of the strain imposed upon them by the surrounding living and growing cells. In fact, in some cases they are stretched beyond their limits of elasticity and their longitudinal walls break down, leaving the lignified rings or portions of spirals in a cavity which is called a lysigenous cavity. This is often seen in monocotyledonous bundles (see Fig. 82).

The first-formed elements of the phloem form the protophloem which occupies the outermost part of the phloem. These are simple elongated, vacuolated, thin-walled cells, capable of longitudinal and tangential extension, but becoming narrower as this proceeds, until ultimately the tangential (periclinal) walls almost touch and the cells are said to have collapsed. The metaphloem and metaxylem differentiate in the region where growth in length has ceased. Their walls are elastic, but in the case of the metaxylem not nearly so extensible as the preformed elements.

Differentiation in each desmogen strand is therefore downward and inward (Fig. 65), ultimately leaving a layer of meristematic tissue across the middle of each bundle. This, as we have already indicated, is known as the cambium. It separates the phloem, external to it, from the xylem inside it. Not only so, but later, cambium formation spreads across the primary medullary rays. Certain medullary ray cells divide by two parallel tangential walls, giving rise to three cells of which the middle one is a cambial cell. The bundle cambium is called fascicular, and the medullary ray cambium interfascicular. The two together form a continuous ring round the stem, but the former is strictly a primary, and the latter a secondary meristem.

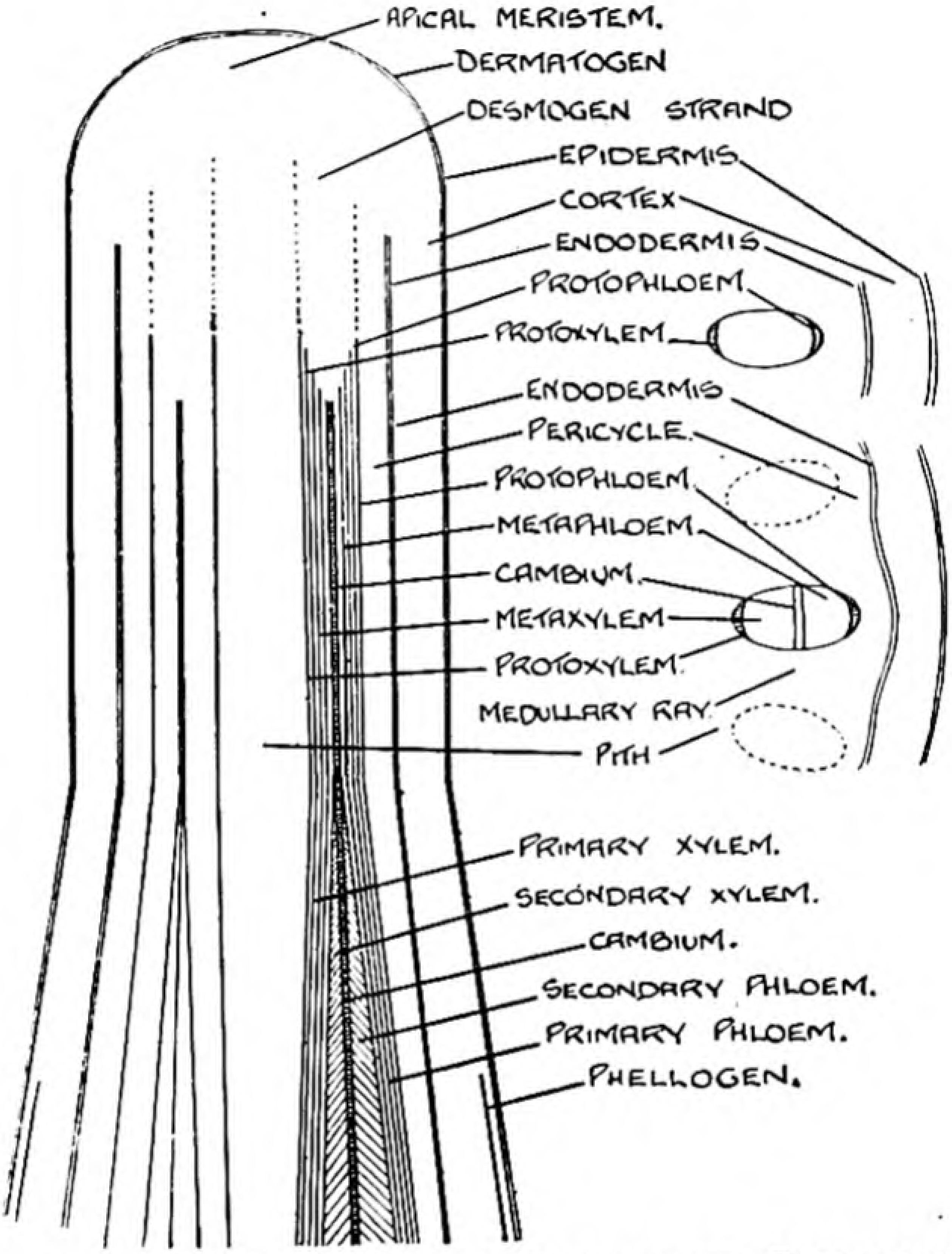

APICAL MERISTEM.
DERMATOGEN
DESMOGEN STRAND
EPIDERMIS
CORTEX
ENDODERMIS
PROTOPHLOEM
PROTOXYLEM
ENDODERMIS
PERICYCLE
PROTOPHLOEM
METAPHLOEM
CAMBIUM
METAXYLEM
PROTOXYLEM
MEDULLARY RAY
PITH
PRIMARY XYLEM.
SECONDARY XYLEM.
CAMBIUM.
SECONDARY PHLOEM.
PRIMARY PHLOEM.
PHELLOGEN.

Fig. 65. Diagram Representing Progressive Differentiation Behind the Stem-apex.

In studying the various tissues and the elements of which they are composed it is necessary to see them not only in transverse section but also in longitudinal section. For this purpose the student should cut radial longitudinal sections of the internode of the sunflower or artichoke stem and treat as for the transverse sections. A true radial section should be along a radius of the circle of the stem. For vascular bundle structure the radius should, of course, pass through the bundle (Fig. 66). In such a true radial section the order of the arrangement of the tissues will be the same as in the transverse section, and it is important to be able to correlate the two views for a proper understanding of these tissues. Even so, our conception still is not complete, for it is necessary also to cut other sections along the chord of the circle at right angles to the radius through each tissue in turn. Such sections are described as tangential, but they are only truly tangential in the region where the chord cuts the radius. From transverse, radial and tangential sections it is possible to build up a complete conception of a tissue, and of the elements which compose it, in the solid, as though they were isolated from the other tissues. Tissue-elements can actually be isolated for purposes of micro-examination by using macerating fluids such as a mixture of potassium chlorate and fuming nitric acid, or 5% potassium hydroxide solution. These destroy the middle lamellae and thus permit the separation of individual cells from each other.

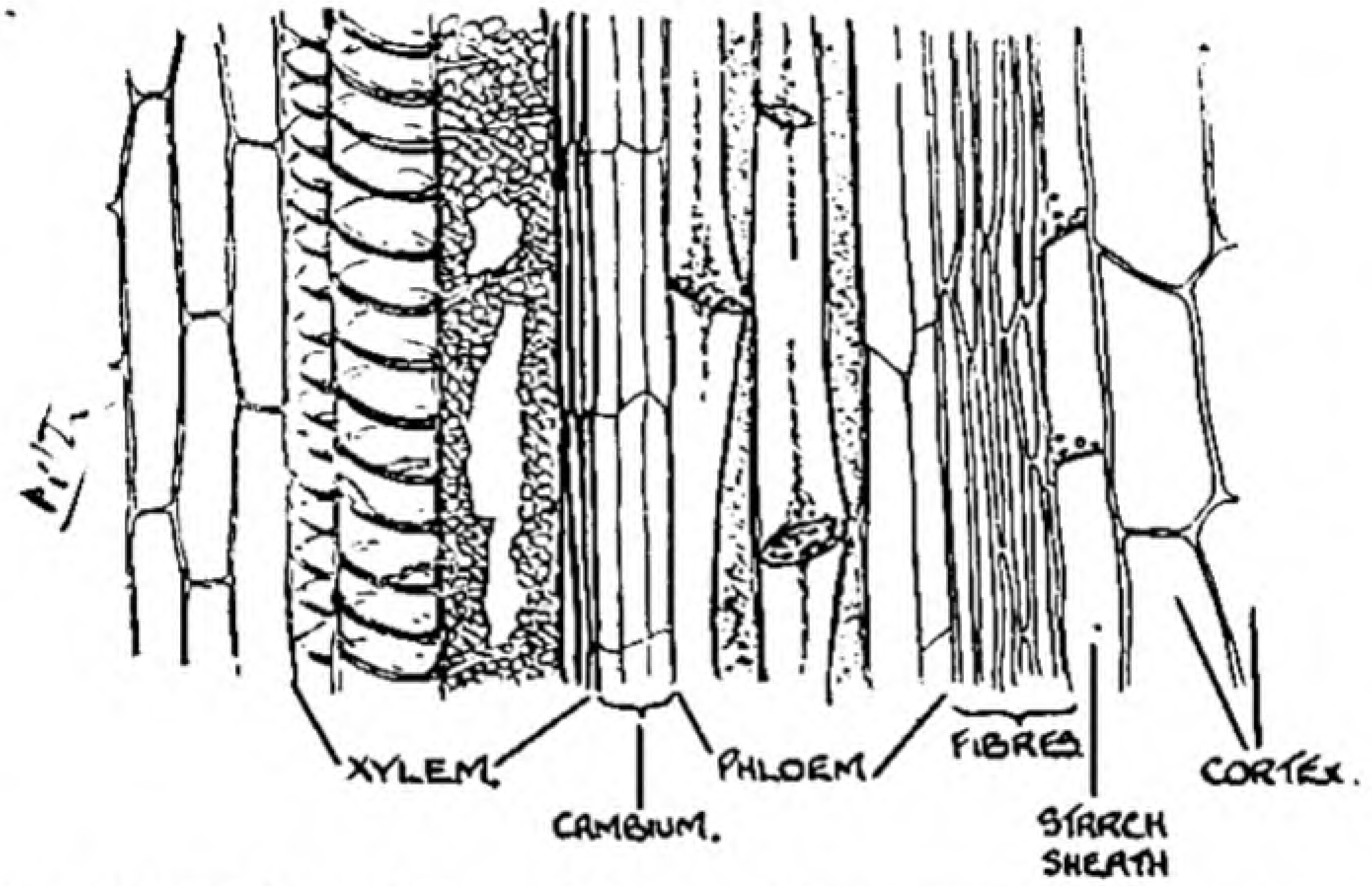


Fig. 66. *Helianthus*, STEM: RADIAL LONGITUDINAL SECTION, DETAIL.

So far we have confined our attention to one example of a dicotyledonous stem. If other examples are studied, it will be found that whilst the fundamental arrangement consists of epidermis, narrow cortex, starch-sheath, a ring of open vascular bundles separated by medullary rays and a large pith, there is considerable diversity resulting from the distribution of such tissues as collenchyma and sclerenchyma. In some instances these tissues may be absent, or, if present, sclerenchyma may form a part of the cortex, it may even be present as part of the epidermis, it may form a continuous girdle in the pericycle, it may form a bundle to the inside of the protoxylem, it may completely surround a vascular bundle, or it may form a bridge across the medullary rays connecting the metaxylem regions of the ring of bundles.

If the student learns to recognise the various tissues by the structure of their tissue elements, he will have no difficulty in interpreting the structure of any organ of the plant. There is no such thing as a single "type" structure which can be memorised to serve for all cases. There is great diversity in Nature, and each case must be taken on its own merits.

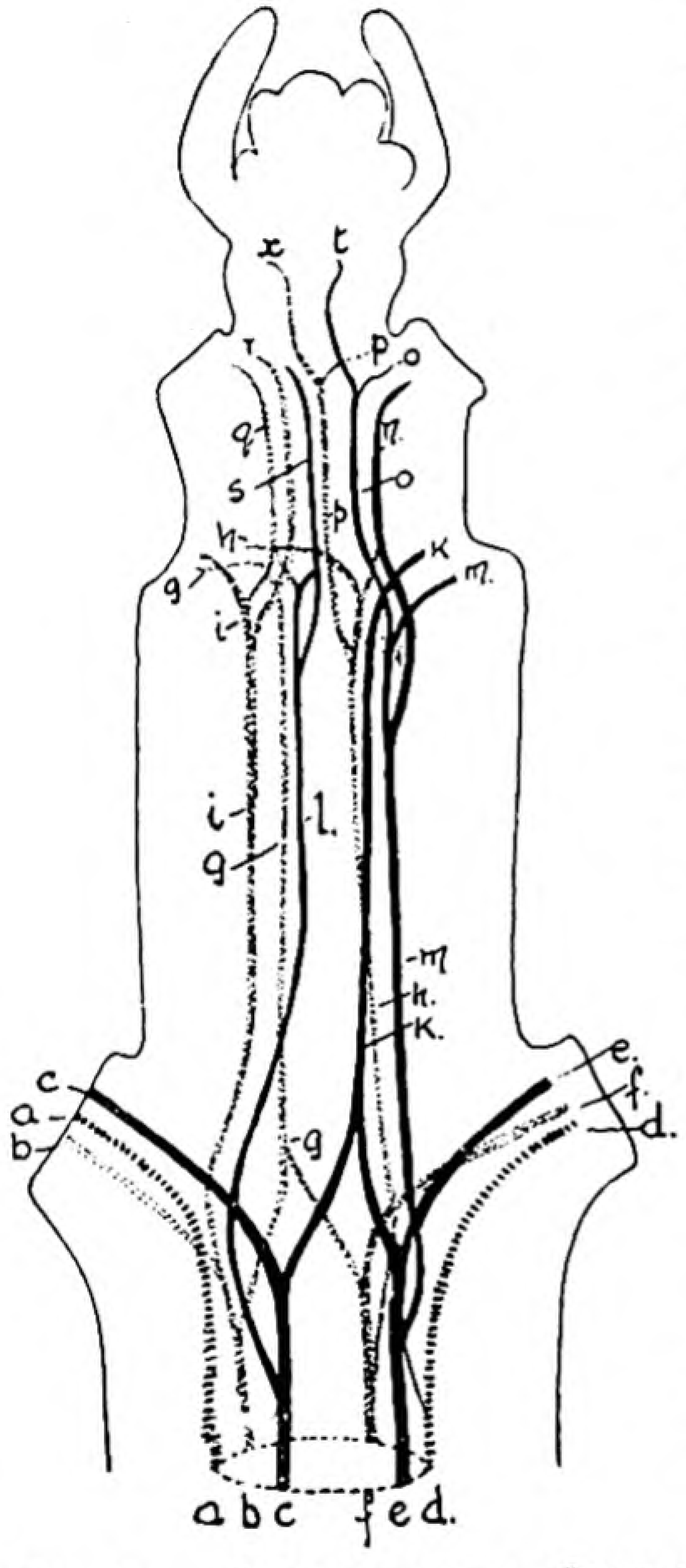


Fig. 67. LONGITUDINAL COURSE OF VASCULAR BUNDLES IN STEM OF *Clematis viticella*.

14. Longitudinal Course of the Bundles

Fig. 67 represents diagrammatically the longitudinal course of the bundles in *Clematis viticella*, a Dicotyledon which has a decussate arrangement of its leaves. Each leaf-trace consists of a median and two lateral strands. The median strand, entering the stem at a node, travels down one internode and forks at the next node. The limb of each fork coalesces with a lateral strand of the leaf-trace at this node. Also the lateral strands from the node above fuse with these lateral strands. A transverse section through an internode therefore shows six vascular bundles.

The bundles are common bundles, *i.e.* they are not confined to the stem, but are common to stem and leaf. The upper part of the bundle, running obliquely through the cortex towards the leaf, is called the **leaf-trace**. In the stem all the bundles run parallel to the epidermis, and at an equal distance from it. That is why, in transverse section, they form a ring. There is frequently considerable branching and intercommunication of the bundles at the nodes. It follows that the primary medullary rays are of limited height. The leaf-trace bundle arises independently in the exogenous outgrowth of cells which, in the course of their development ultimately take shape as a leaf (Fig. 32). Differentiation of the elements of the bundle proceeds upwards into the developing leaf and downwards into the stem.

In the stems of a few Dicotyledons *cauline bundles, i.e.* bundles confined to the stem, are found in addition to the usual common bundles. They usually run through the pith within the ring of common bundles and communicate with the latter at the nodes. There are also some Dicotyledons in which the vascular bundles form two (e.g. *Cucurbita*, *Bryonia*) or more (*Thalictrum*, *Papaver*) rings.

15. Distribution of Strengthening Tissue

It will be observed that the strengthening tissues in the dicotyledonous stem (xylem, sclerenchyma, collenchyma) are arranged near the periphery. This arrangement best meets the strains to which the stem is subject. A little reflection will show that the stem of a land-plant is mostly subject to bending strains (from wind and other influences). Now, if we bend a stem, it will be evident that the strain falls chiefly on the two sides of the stem. On the concave side the outer tissues will be compressed, while on the convex side they will be elongated. There is little or no strain in the middle. Thus the strengthening tissue will be most advantageously disposed near the periphery where the strain is greatest.

In roots, stems of water-plants, and other members, which must be able to bend and yet withstand pulling strains, the strengthening tissue, as we shall see later, is arranged in the centre. It may be taken as a general rule that the distribution of strengthening tissue in the various parts of a plant is related to the strains to which they are subject.

16. Summary

The stems of most herbaceous Dicotyledons, and the young shoots of dicotyledonous shrubs and trees, have a structure agreeing in its general characters with that just described. These general characters may be summarised—

(*a*) The apical meristem shows, more or less distinctly, dermatogen, periblem, and plerome.

(*b*) The bundles, in transverse section, are arranged in a ring, and are separated by the parenchymatous medullary rays.

(*c*) The bundles are collateral, occasionally bi-collateral, and most of them common. The xylem usually contains vessels, tracheides, wood-fibres, and wood parenchyma. The phloem contains sieve-tubes, companion cells, and phloem parenchyma.

(*d*) The bundles are open, and secondary growth may take place.

(*e*) There is a relatively large pith, usually parenchymatous.

(*f*) The cortex is relatively narrow and may contain collenchyma and parenchyma. Its inner limit is the starch-sheath.

(*g*) The pericycle may consist of parenchyma, and often also sclerenchymatous fibres, either in groups outside the vascular bundles or as a continuous layer surrounding the stele.

(*h*) The epidermis is normally a single layer of cells and may contain stomata and bear hairs of various types.

17. Other arrangements in Dicotyledons

In the stems of the marrow family (Cucurbitaceae), there are often two rings of bicollateral bundles (Fig. 68). Internal (perimedullary) phloem is also present in the stems and leaf-bundles of members of the family Solanaceae.

18. Secondary Growth

We have now described the *primary* structure characteristic of dicotyledonous stems. In herbaceous Dicotyledons it is often the only structure to be recognised. On the other hand, in those perennial Dicotyledons whose aerial parts continue their growth from year to year, and which form shrubs and trees, this primary structure is completely modified by **secondary growth** which provides for the necessary extension of the vascular and other systems of tissue. By secondary growth is meant the formation of new tissue owing to the activity of a cambium layer, so that the part in which it occurs increases in thickness.

The student must bear in mind that the cambium is a meristem. Its cells are capable of dividing and forming new cells, which are modified or differentiated into permanent tissue-elements. The new tissues thus formed are called *secondary* to distinguish them from the tissues differentiated from the apical meristem. In considering this process we have to study the formation, not only

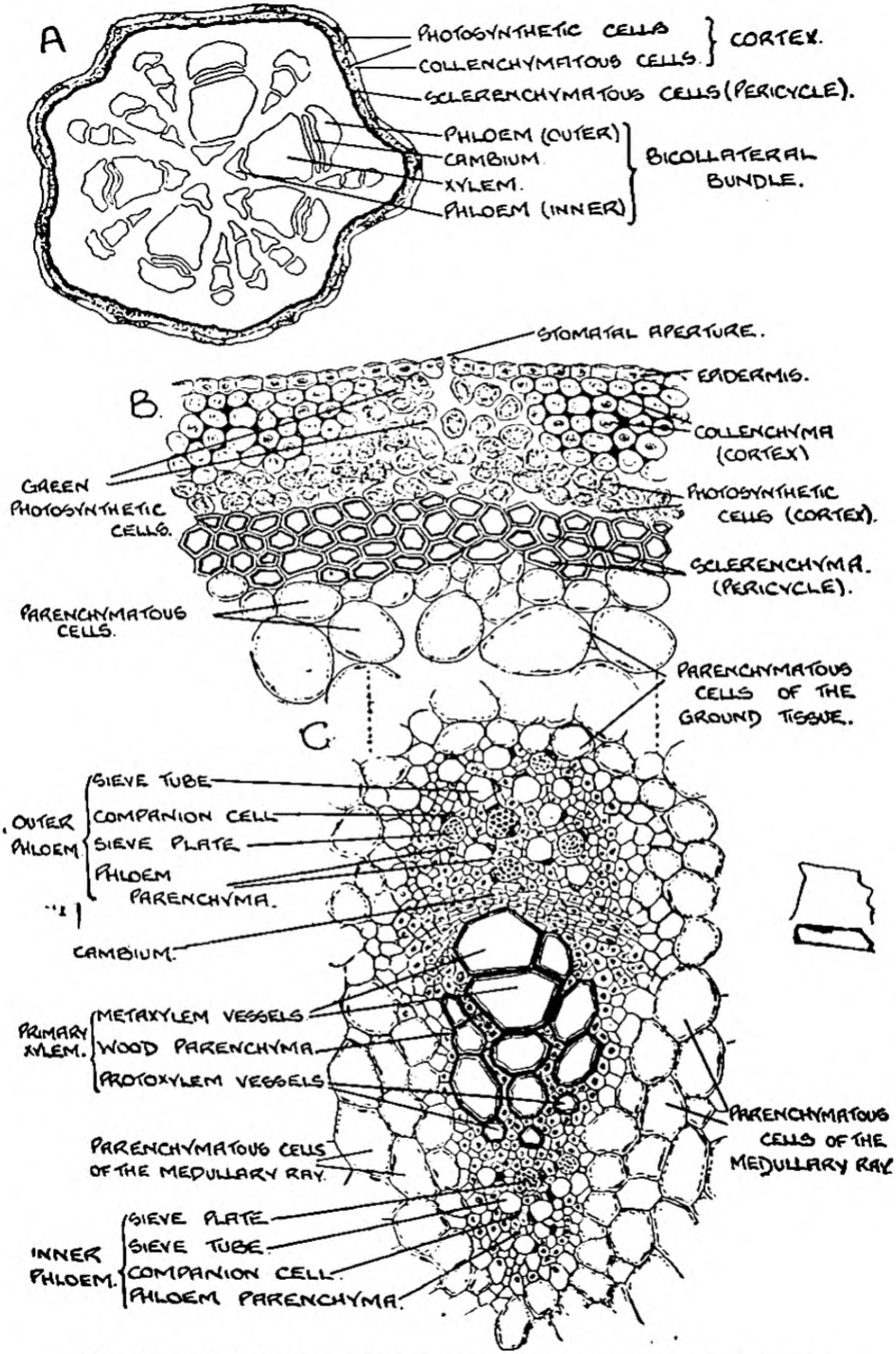

A
PHOTOSYNTHETIC CELLS
COLLENCHYMATOUS CELLS
CORTEX.
SCLERENCHYMATOUS CELLS (PERICYCLE).
PHLOEM (OUTER)
CAMBIUM
XYLEM.
PHLOEM (INNER)
BICOLLATERAL BUNDLE.
STOMATAL APERTURE.
B.
EPIDERMIS.
COLLENCHYMA (CORTEX)
GREEN PHOTOSYNTHETIC CELLS.
PHOTOSYNTHETIC CELLS (CORTEX).
SCLERENCHYMA. (PERICYCLE).
PARENCHYMATOUS CELLS.
PARENCHYMATOUS CELLS OF THE GROUND TISSUE.
C.
OUTER PHLOEM
SIEVE TUBE
COMPANION CELL
SIEVE PLATE
PHLOEM PARENCHYMA.
CAMBIUM.
PRIMARY XYLEM.
METAXYLEM VESSELS
WOOD PARENCHYMA
PROTOXYLEM VESSELS
PARENCHYMATOUS CELLS OF THE MEDULLARY RAY.
PARENCHYMATOUS CELLS OF THE MEDULLARY RAY
INNER PHLOEM.
SIEVE PLATE
SIEVE TUBE
COMPANION CELL
PHLOEM PARENCHYMA

Fig. 68. *Bryonia* STEM (CUCURBITACEAE), TRANSVERSE SECTION.
A, Diagrammatic; B, Detail.

]

of secondary vascular tissue, but also of secondary ground-tissue (phelloderm) and secondary tegumentary tissue (cork).

19. Initiation of the Process

We have already seen that there is a layer of fascicular cambium between the primary xylem and phloem and also that certain of the parenchymatous cells in each medullary ray become meristematic to form the **interfascicular cambium.** In this way a complete ring of cambium—the **cambium ring**—is formed in the stem. Its formation can readily be studied in the older internodes of *Helianthus*, where there are the beginnings of secondary growth, or in the young green twigs of trees.

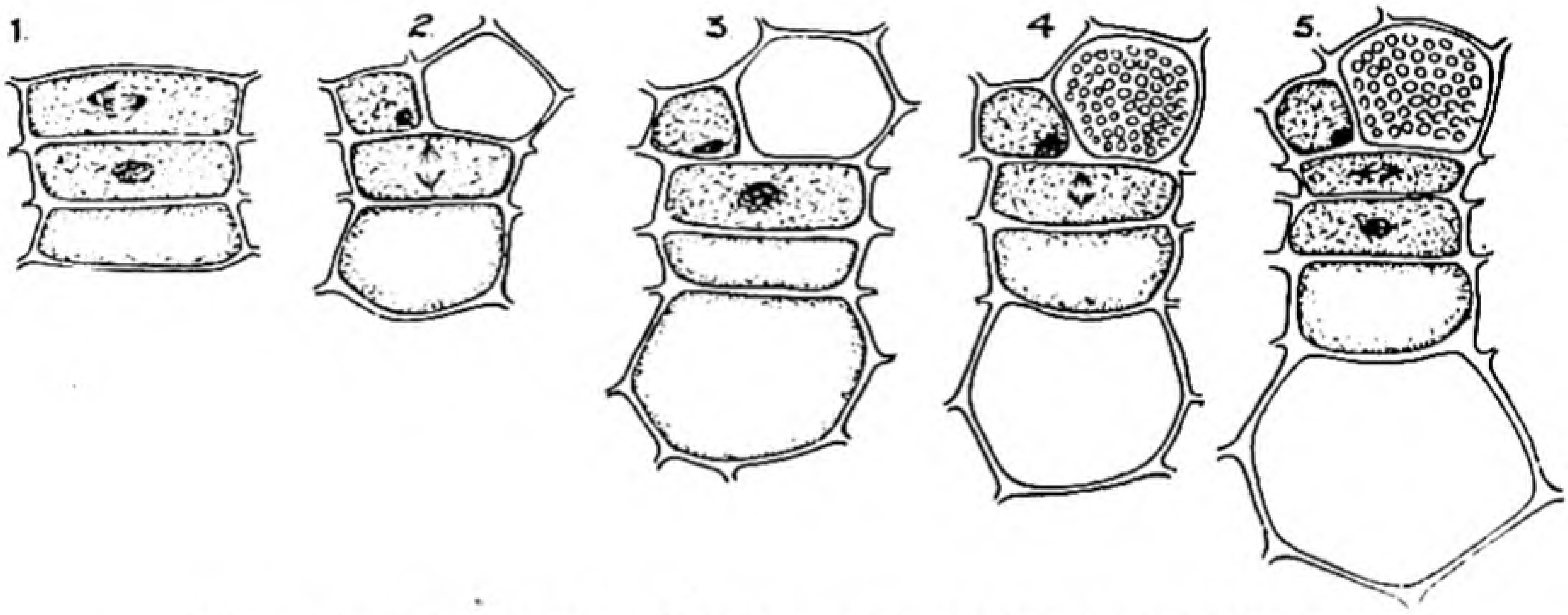


Fig. 69. Cambium: Origin and Division as seen in Transverse Section.

20. Division of the Cambial Cells (Fig. 69)

The elongated cambium cells are flattened in the radial direction, a[illegible]r end-walls are obliquely inclined (Fig. 4). The method of divisi[illegible] as follows: Each cell divides *tangentially* (*i.e.* by a wall at right angles to the radial direction) into an outer cell and an inner cell. Of these one continues as a cell of the cambium. The other may divide once or twice, but the cells to which it gives rise are ultimately differentiated into permanent tissue. The cell which continues as a cambial cell increases in size and again divides. As before only one of the two cells is differentiated. Sometimes it is the cell to the inside of the cambial cell which differentiates as a xylem element, sometimes the cell to the outside becomes a phloem element. In this way the amounts of xylem and phloem are increased, whilst in between them the cambium remains as a permanent meristem.

21. The Secondary Tissues (Fig. 70)

Since the fascicular cambium is present and active before the interfascicular cambium is completely formed, it follows that secondary xylem and phloem will first appear between the primary xylem and phloem of the vascular bundles, and will have developed to some extent before the interfascicular cambium has completely bridged the medullary ray and the entire ring of fascicular and interfascicular cambium is functioning. At the time this stage is reached, the xylem is roughly in the form of a number of wedge-shaped groups whose apices are occupied by the primary xylem groups and whose bases extend along the inside of the cambium ring (Fig. 70, B). In other words, the xylem zone is thinnest at points about midway across each primary medullary ray, where the interfascicular cambium was latest in forming, and thickest along the radii passing through the middle of each original vascular bundle. A transverse section of an internode at this stage of development illustrates clearly the considerable surface-extension of the cambial ring. In order to cope with this continually increasing surface the cambial cells must divide by radial walls occasionally, and the two cells thus formed must enlarge in the tangential plane, each to the size of the original parent cell.

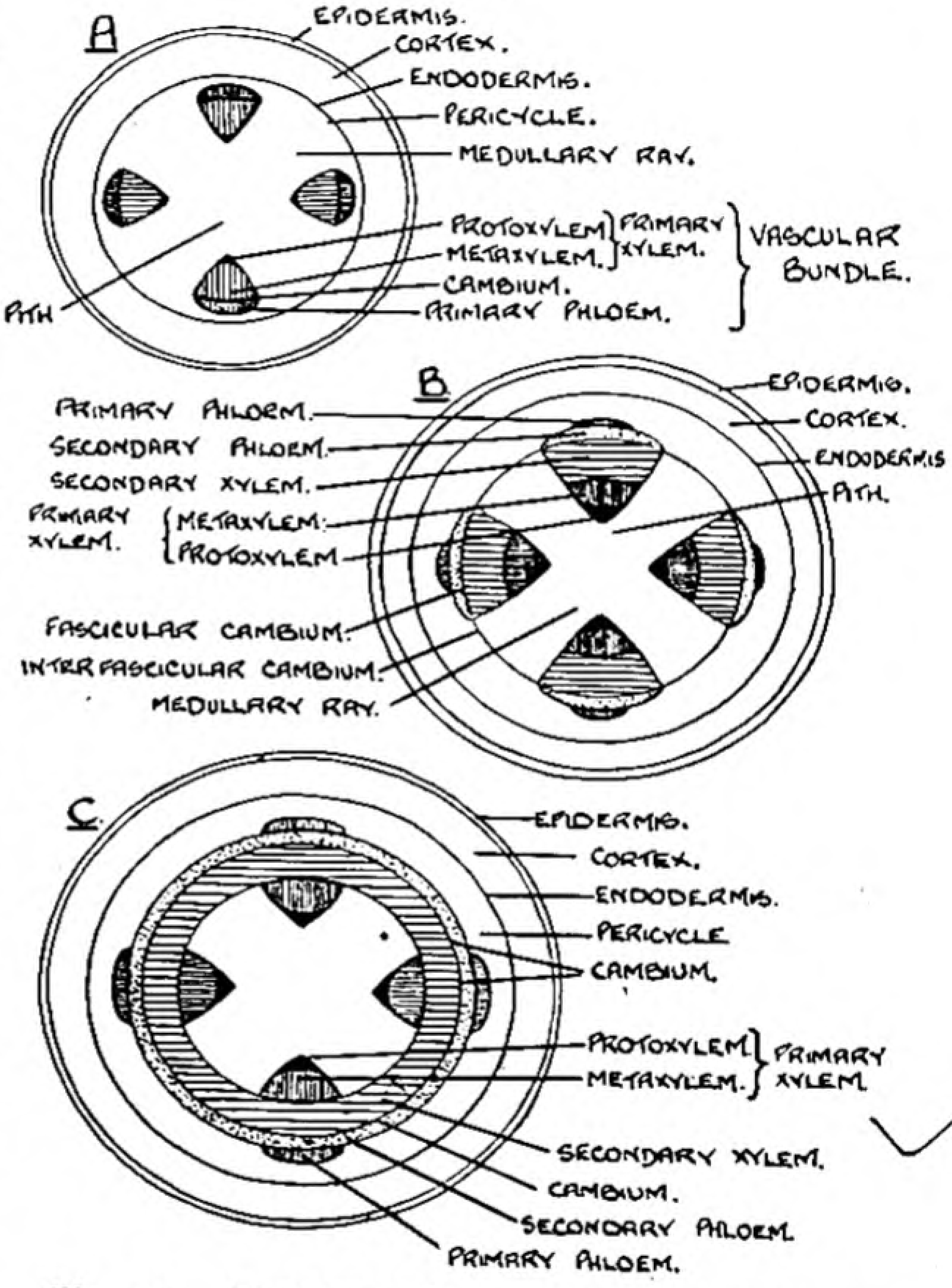

A
EPIDERMIS.
CORTEX.
ENDODERMIS.
PERICYCLE.
MEDULLARY RAY.
PROTOXYLEM
METAXYLEM.
PRIMARY XYLEM.
VASCULAR BUNDLE.
CAMBIUM.
PRIMARY PHLOEM.
PITH
B
PRIMARY PHLOEM.
SECONDARY PHLOEM.
SECONDARY XYLEM.
PRIMARY XYLEM.
METAXYLEM.
PROTOXYLEM
FASCICULAR CAMBIUM.
INTERFASCICULAR CAMBIUM.
MEDULLARY RAY.
EPIDERMIS.
CORTEX.
ENDODERMIS
PITH.
C
EPIDERMIS.
CORTEX.
ENDODERMIS.
PERICYCLE
CAMBIUM.
PROTOXYLEM
METAXYLEM.
PRIMARY XYLEM
SECONDARY XYLEM.
CAMBIUM.
SECONDARY PHLOEM.
PRIMARY PHLOEM.

Fig. 70. Diagrams Illustrating Stages in Secondary Thickening of a Stem.

The repeated tangential division of the cells of the cambium ring results in increased secondary xylem formation inside it. Therefore the distance of the cambium from the centre of the stem must slowly increase. But we also have secondary phloem resulting from the differentiation of cells formed from the divisions of the cambial cells outwards. Hence the primary phloem groups are pushed further and further out and at the same time spread out on the circumference of an ever widening circle. They are subjected to lateral tension and after a time are no longer recognisable as distinct groups. Bundles of sclerenchymatous fibres, forming the external portion of the original fibro-vascular bundles, persist as scattered groups on the periphery of the secondary phloem. The starch sheath loses its distinctive characters, and the cortical cells become stretched tangentially as secondary increase in thickness proceeds. The epidermis also is subjected to increasing strain, which gradually impairs its function as a protective layer, and in order to compensate for its loss another secondary meristem, the **phellogen** or **cork-cambium** arises in the outer region of the stem and produces an entirely new protective layer, the **periderm.** We shall return to this later.

Since the interfascicular cambium as well as the fascicular produces this secondary tissue, there are no longer *wide* medullary rays running between pith and cortex. Certain cells of the cambium ring, however, instead of giving rise to xylem and phloem elements, produce parenchymatous cells which form narrow medullary rays traversing radially the secondary xylem and phloem. Strictly speaking, because they are formed from the cambium, they consist of secondary tissue. Usually, however, those few rays, although now very narrow, which continue the course of the wide, original primary rays from pith to cortex are still called primary rays. The term secondary is reserved for those whose formation began later, and which therefore start somewhere in the secondary xylem and end somewhere in the secondary phloem.

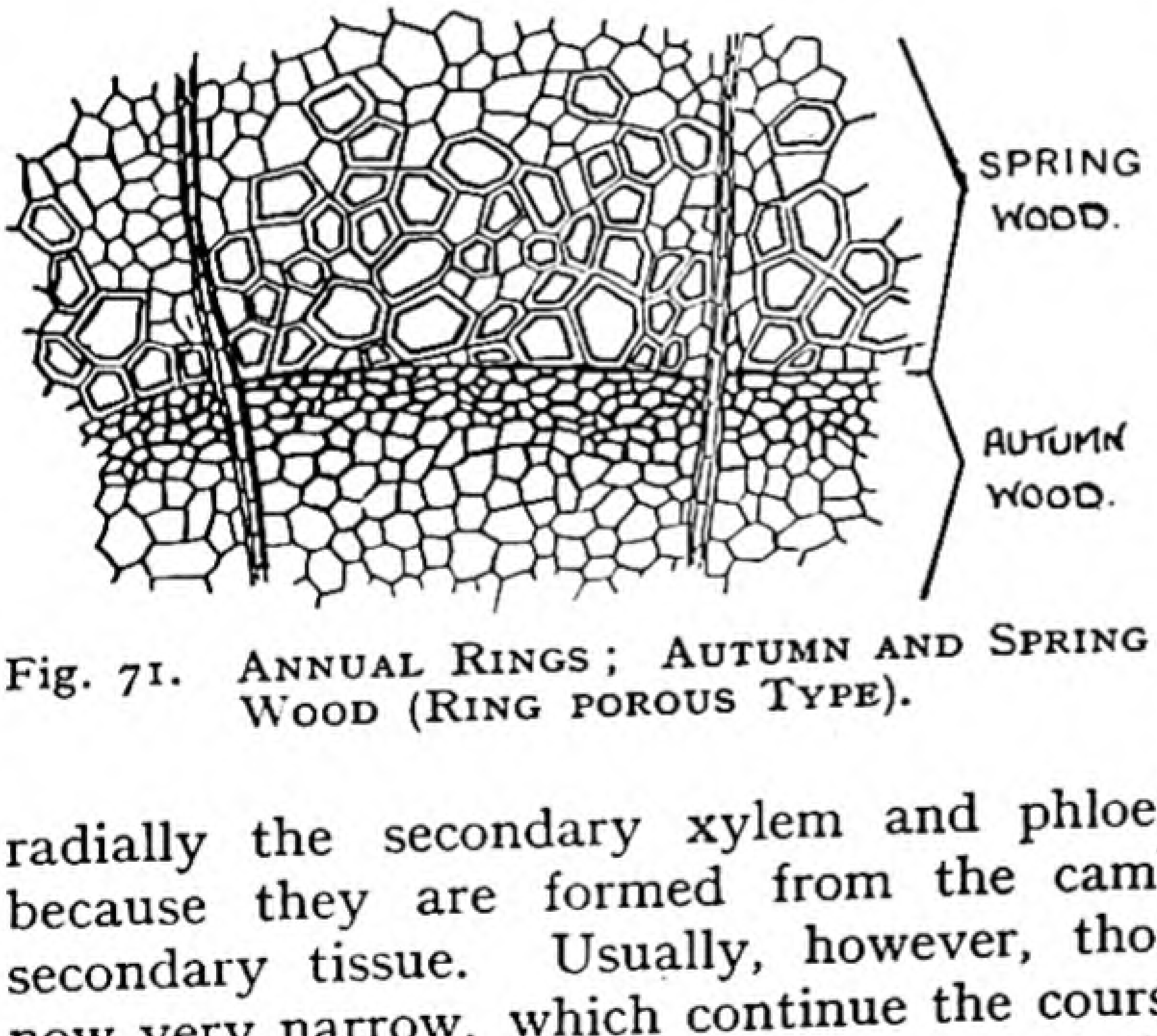


Fig. 71. ANNUAL RINGS; AUTUMN AND SPRING WOOD (RING POROUS TYPE).

22. Annual Rings (Fig. 71)

In cool temperate climates the cambium ceases its activity during the winter and renews it in the spring. The exact causes leading to the renewal of cambial activity in the spring are not known, but it is probable that bud-break precedes cambial activity and that it is the young unfolding leaves which provide the necessary stimulus to the cambium, causing its cells to begin active division. Each year the cambium forms a band of secondary xylem and secondary phloem, and the bands of secondary xylem are clearly marked off from each other, forming **annual rings**: the number of these annual rings in a woody stem gives, of course, a clear indication of its age.

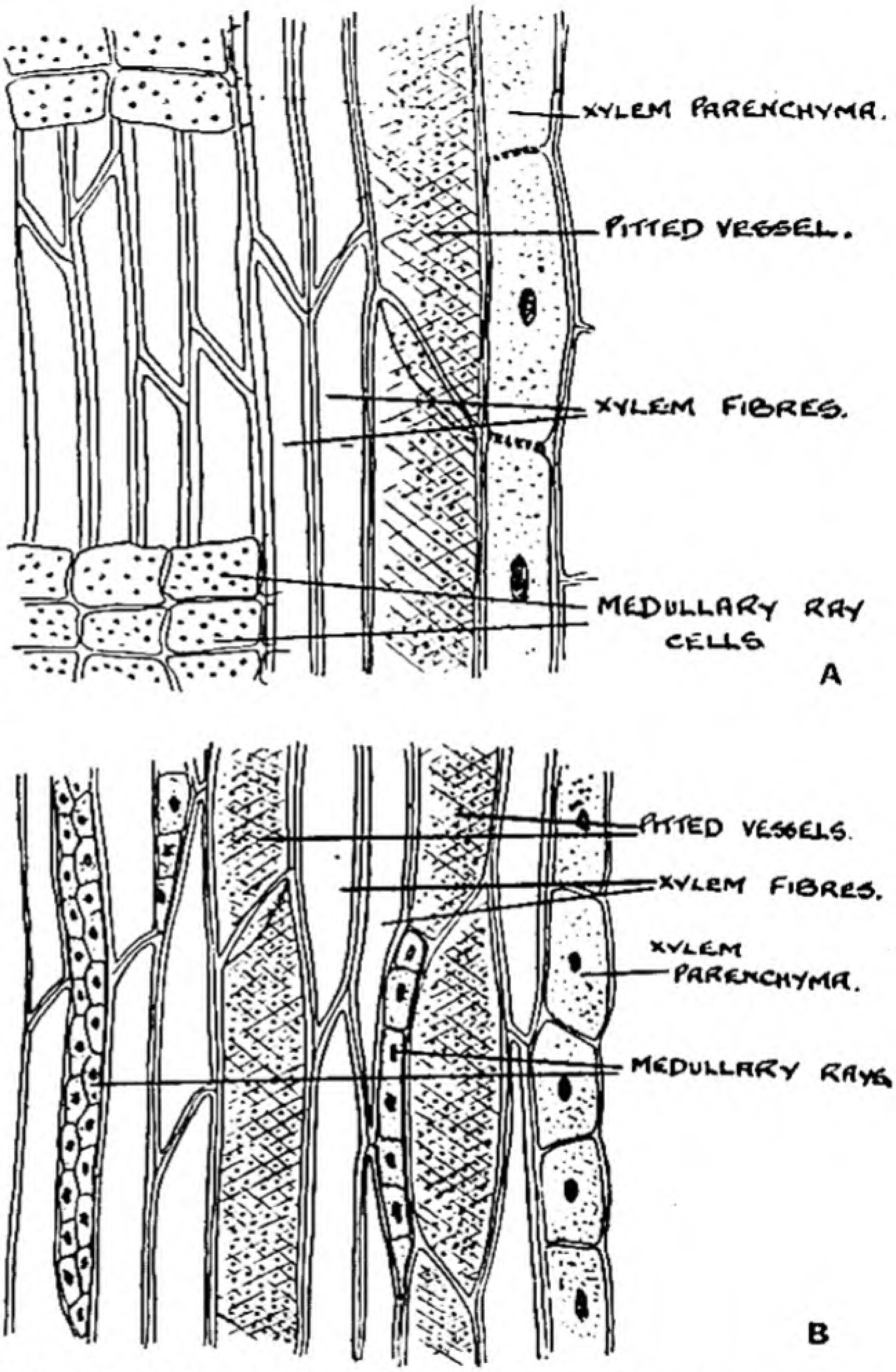


Fig. 72. STRUCTURE OF SECONDARY XYLEM OF LIME. A, Radial ; B, Tangential longitudinal sections.

23. Spring and Autumn Wood

The xylem formed in the spring differs somewhat from that formed in the autumn. The former, the **spring wood,** consists of large elements and the **autumn wood** of smaller, more strongly thickened elements. The causes of this are not clear, but possibly the spring wood is formed at a time when the water-supply is good, so that cell extension is encouraged, resulting in the formation of large elements. Whatever the cause, the small, autumn-formed elements abut directly on to the larger elements of the spring wood of the following year, and as a result, the limits of wood production within each year are clearly defined. Occasionally, owing to defoliation or other causes, growth may be arrested for a time, in which case a false annual ring results.

In some tropical trees cambial activity may show a rhythm corresponding with alternating wet and dry seasons so that fairly well-marked " annual " rings occur. Often, however, the variations in the wood corresponding to the alternate wet and dry periods are small so that the ring is poorly defined, and it frequently happens that an evergreen growing in a climate of uniform temperature produces wood in which no rings are evident. The occurrence of the ring is not due entirely to climatic causes, e.g. the English oak when grown in the uniform climate of Java still produces wood showing annual rings. Again, in the tropics especially, more than one ring may be produced in a year. In one case as many as five rings were formed in one year, whilst conversely a cocoa tree at Aden formed only five to six rings in thirty years, but these are exceptional cases.

No rings are generally found in the wood of *Mesua ferrea* (iron wood) or the jak (*Artocarpus integrifolia*). In *Pongamiaglabra* and in the banyan (*Ficus bengalensis*) false rings consisting of alternating bands occur, but no true annual rings are present. Annual rings are present but poorly defined in *Albizzia* and *Heritiera*, but are well defined in *Tecoma grandis* (teak), *Dalbergia* and *Shorea*.

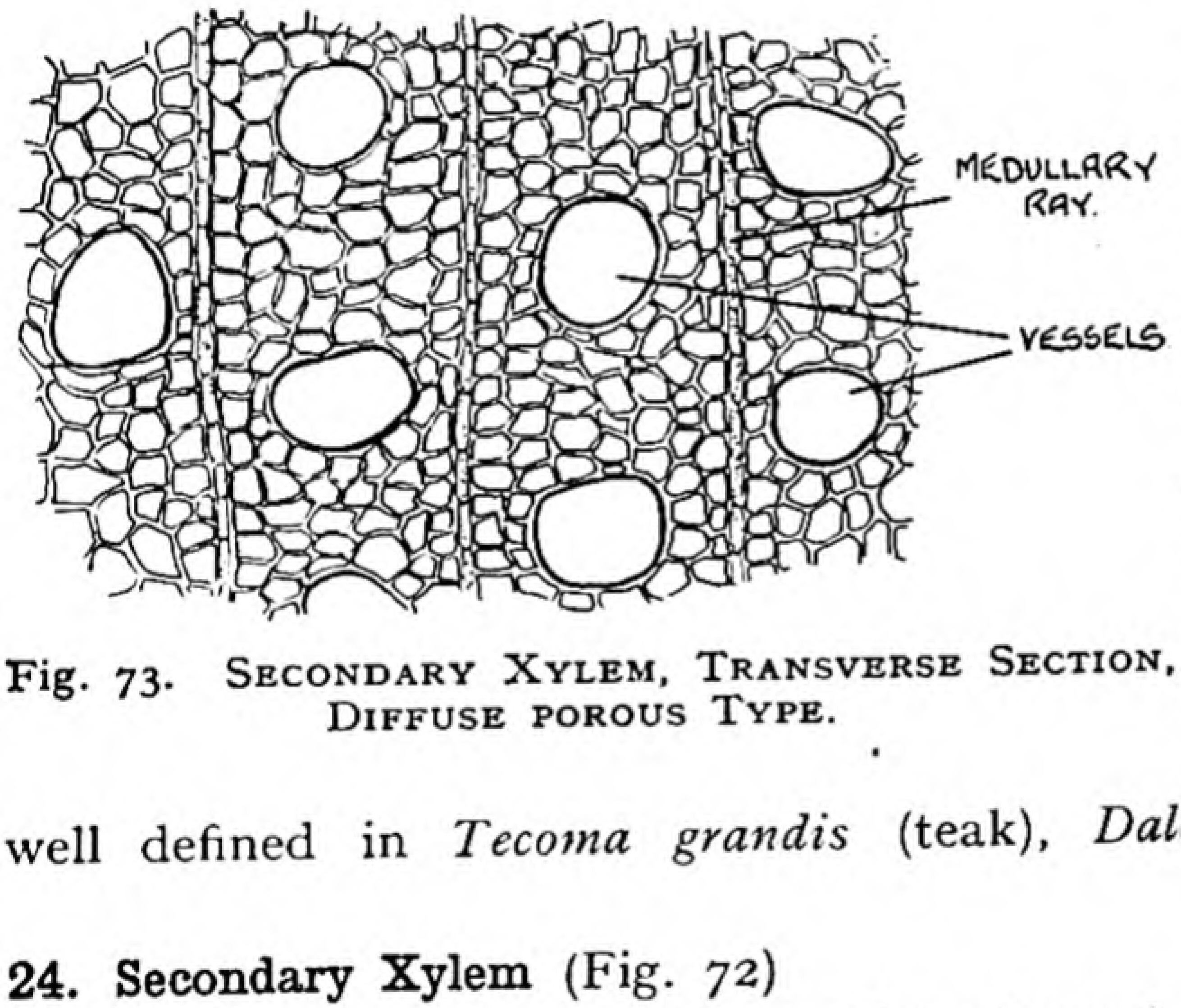


Fig. 73. SECONDARY XYLEM, TRANSVERSE SECTION, DIFFUSE POROUS TYPE.

24. Secondary Xylem (Fig. 72)

The *secondary xylem* may consist of wood vessels, tracheides, fibres (sclerenchyma) and parenchyma. Only the last mentioned have living contents. All the vessels are pitted, as also are the tracheides, and the walls of these elements may be further strengthened by spiral or reticulate bands of thickening inside the pitted cell-wall. (These elements must not be confused with protoxylem elements.) The wood parenchyma usually contains abundant starch, and appears to serve as a storage tissue. The fibres are purely mechanical in function, but the vessels and tracheides whilst also serving this function by virtue of their thick lignified walls primarily serve as channels through which water and dissolved substances are transported from the roots to the leaves.

The distribution of large vessels in the secondary wood may follow a definite pattern according to the species of tree. Sometimes they are scattered irregularly throughout the xylem, giving what is described as a diffuse porous wood (e.g. *Populus*, *Betula*, *Pyrus Malus*) (Fig. 73), or arranged more regularly in rings corresponding with the spring wood, as in ring porous wood (e.g. *Quercus*, *Fraxinus*) (Fig. 71).

25. Secondary Phloem (Fig. 74)

The *secondary phloem*, as seen in transverse section, usually forms a continuous circular band traversed by medullary rays. Some of the latter tend to widen out towards the exterior of the phloem, either owing to tangential expansion, or to the division of their cells. The phloem may consist entirely of soft bast (sieve-tubes, companion cells and phloem parenchyma), but sometimes it contains hard bast (sclerenchymatous fibres) as well, as in lime. The function of the phloem parenchyma is not well understood, but in its cells nitrogenous

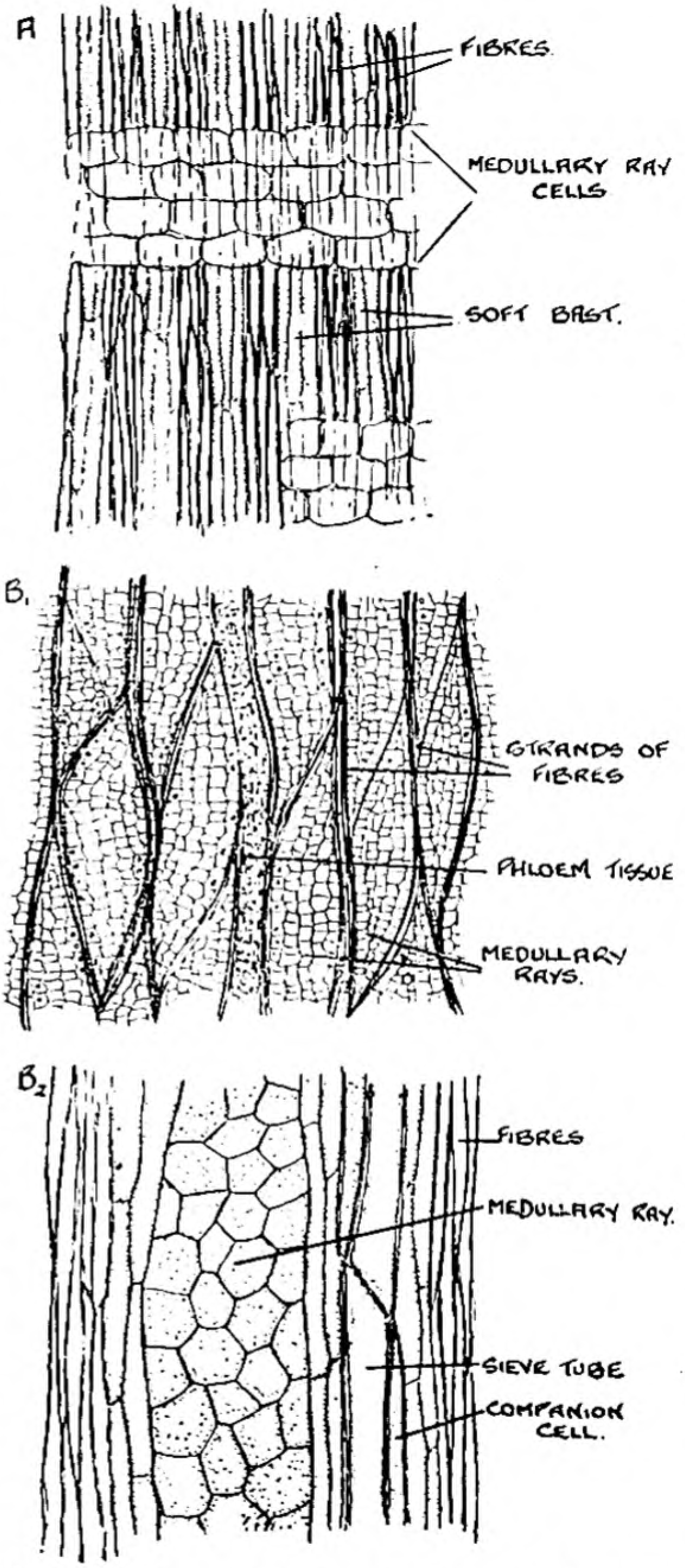

A
FIBRES.
MEDULLARY RAY CELLS
SOFT BAST.
B₁
STRANDS OF FIBRES
PHLOEM TISSUE
MEDULLARY RAYS.
B₂
FIBRES
MEDULLARY RAY.
SIEVE TUBE
COMPANION CELL.

Fig. 74. STRUCTURE OF SECONDARY PHLOEM OF LIME.

A, Radial ; B_1, Tangential sections ; B_2, Magnified for detailed structure.

compounds are often abundant, and probably they are temporarily stored there. Through the sieve-tubes, soluble carbohydrates, especially sucrose, and organic nitrogenous compounds, are transported to regions where active growth is taking place, e.g. the growing points of the main stem and branches, and of the roots, or to the storage organs.

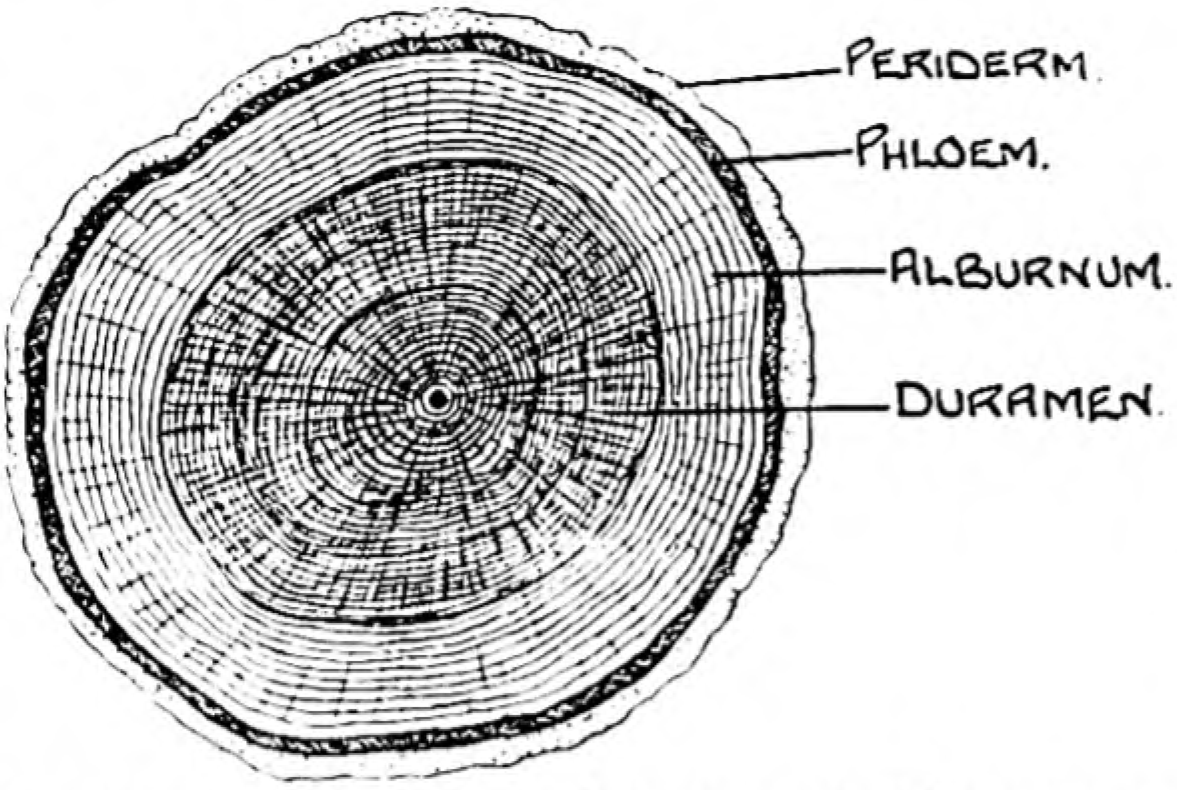


Fig. 75. TRANSVERSE SECTION OF BRANCH OF *Fraxinus*, DIAGRAMMATIC, SHOWING HEART- AND SAP-WOOD.

26. Medullary Rays

The *medullary rays* traverse the xylem and phloem in a radial direction. Their cells are usually elongated radially, but in the outer parts of the phloem they may be elongated tangentially. As seen in tangential sections each group of medullary ray cells is somewhat biconvex lens-shaped in outline, varying from one to a few cells wide, and from two to about fifteen cells high. The cells appear rounded in this view, leaving intercellular spaces through which gaseous interchange may take place in the radial direction. Through the medullary ray cells lateral movement of water may take place, but more especially of food materials in the stem, and it is *via* the medullary rays that the living xylem parenchyma cells are supplied with oxygen, and the necessary organic compounds which have been synthesised elsewhere in the plant.

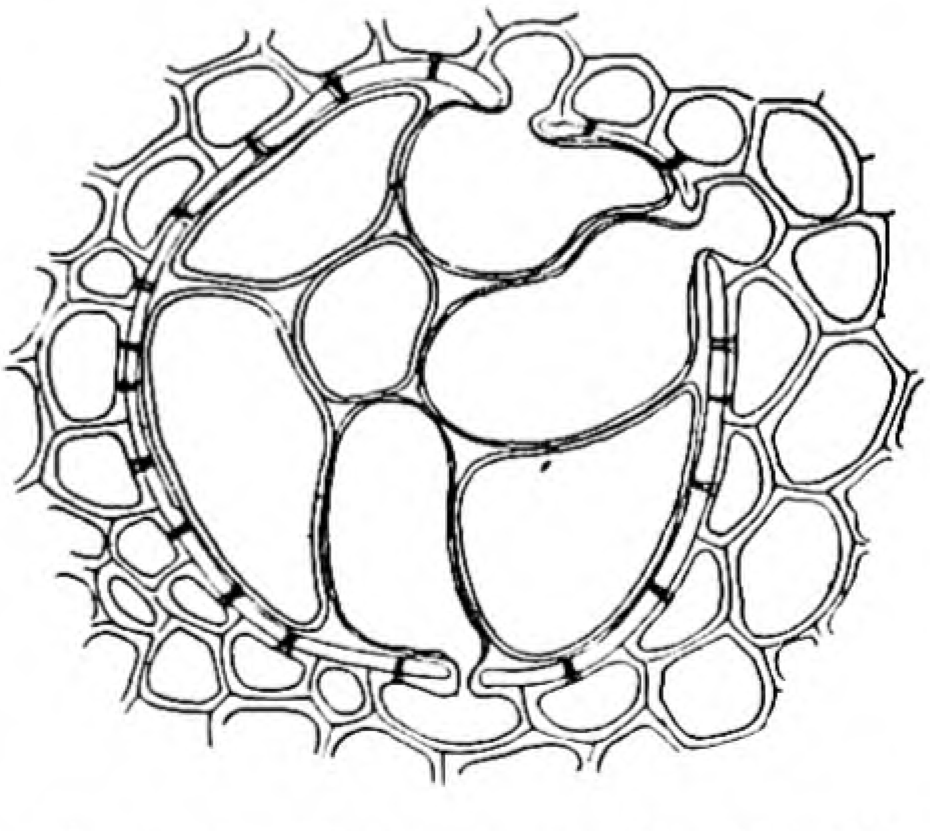


Fig. 76. TYLOSES IN VESSEL OF *Robinia Pseudacacia*.

27. Heart-wood and Sap-wood (Fig. 75)

In the trunk and thicker branches of older trees the central region of the xylem becomes distinctly marked off from the peripheral region. The cavities of the vessels in the central heart-wood or duramen may become blocked by *tyloses*. These are formed by certain of the living cells which surround a vessel expanding in such a way as to intrude through the pits, forcing the pit-closing membrane with them. They enlarge once they penetrate into the cavity of the vessel, and meet similar intrusions from other cells, thus completely blocking the cavity (Fig. 76). Later both wood parenchyma cells and tyloses die, and the elements of the wood become impregnated with resins, tannins and other substances which give a dark colour to the heart-wood and in some cases help to preserve it from decay. Such woods are frequently extremely useful in commerce, either for their durability, their colour and "grain" for ornamental purposes, or even for their medicinal properties.

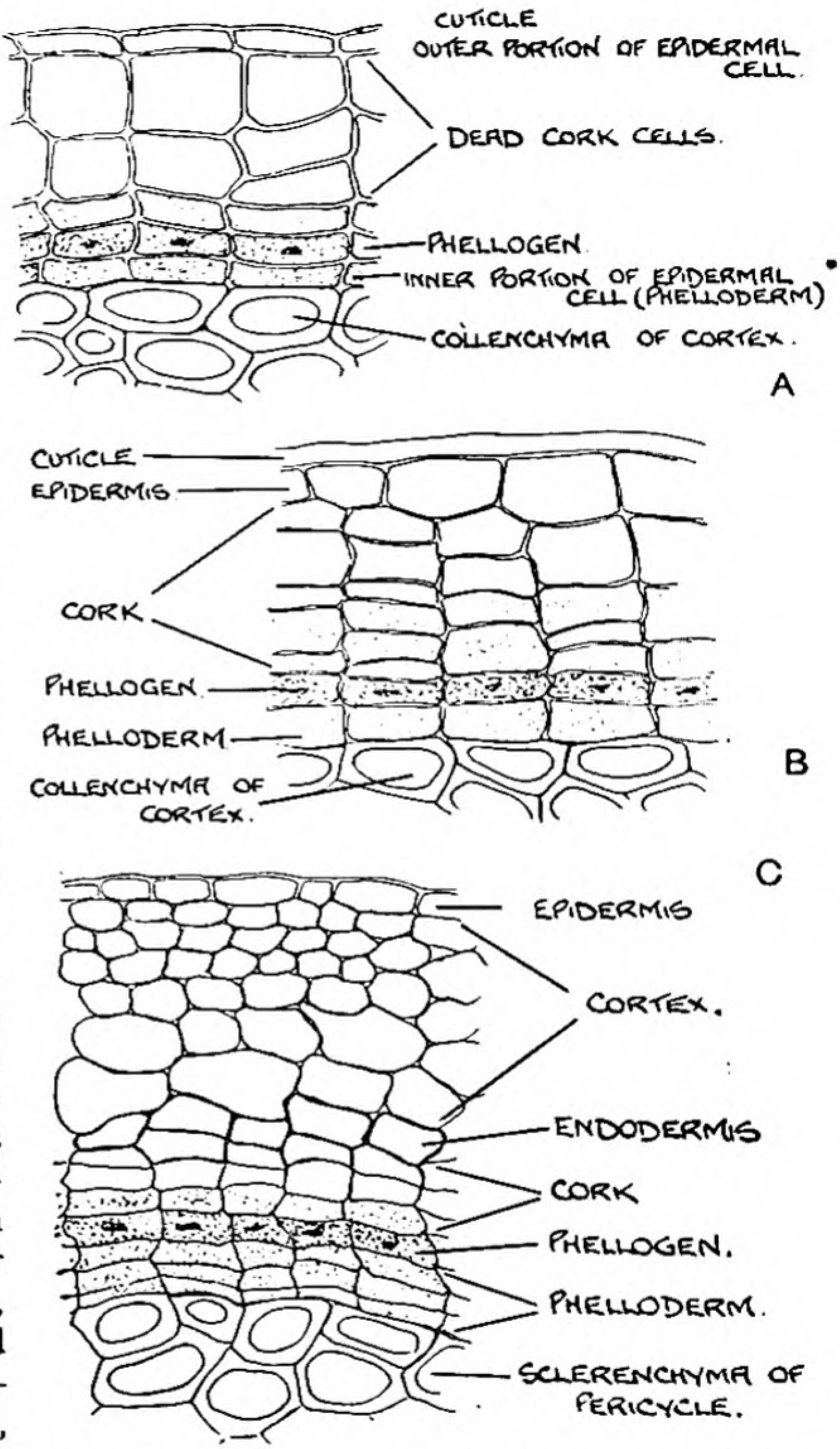

CUTICLE
OUTER PORTION OF EPIDERMAL CELL.
DEAD CORK CELLS.
PHELLOGEN
INNER PORTION OF EPIDERMAL CELL (PHELLODERM)
COLLENCHYMA OF CORTEX.
A
CUTICLE
EPIDERMIS
CORK
PHELLOGEN
PHELLODERM
COLLENCHYMA OF CORTEX.
B
C
EPIDERMIS
CORTEX.
ENDODERMIS
CORK
PHELLOGEN.
PHELLODERM.
SCLERENCHYMA OF PERICYCLE.

Fig. 77. ORIGIN AND DEVELOPMENT OF PHELLOGEN.
A, Epidermal; B, Hypodermal; C, Deep-seated.

The peripheral region of the xylem which alone serves as a channel for water transport is the sap-wood or alburnum. Occasionally, as in beech, almost all the wood is sap-wood, but generally, as a tree gets older, the newer wood functions as sap-wood and the older wood becomes heart-wood. The heart-wood thus increases in amount yearly, as the tree ages.

28. Phellogen—Formation of Cork

We have already noticed that with the formation of secondary vascular tissues the outermost regions of the stem are subjected to tangential stretching. Ultimately they rupture. Very occasionally, as in mistletoe, we find a persistent epidermis which is able to accommodate itself to the increase in bulk of the tissues within. More usually a special protective tissue is formed by the activity of a cambium which arises usually in the peripheral region of the stem. Fully vacuolated cells, either parenchyma or collenchyma, reassume the power of division (cf. interfascicular cambium). They divide by two parallel walls, cutting off an outer and an inner cell to form a middle cambial cell which assumes all the characters of a meristematic cell. The layer of cambial cells thus formed around the stem is called the **cork-cambium** or **phellogen.** It is a secondary meristem.

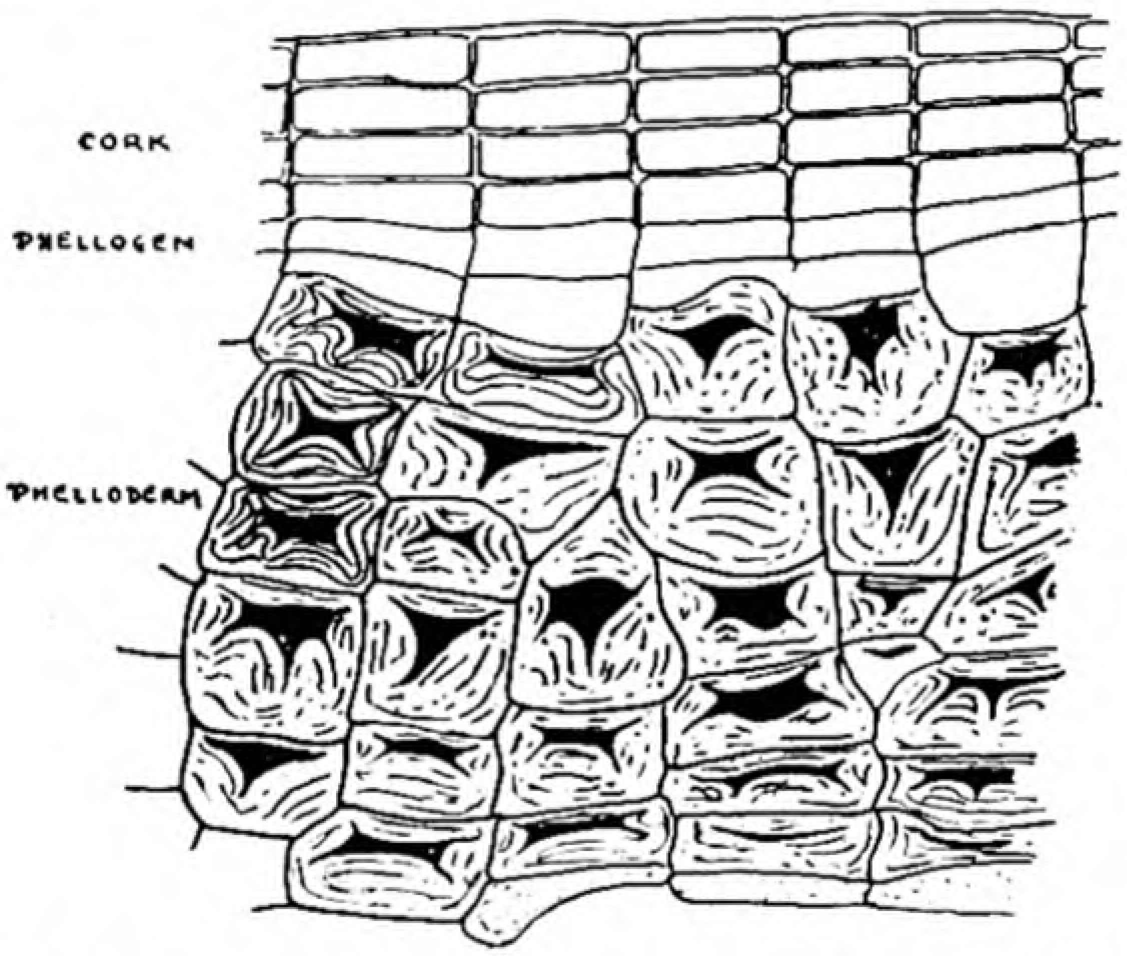


Fig. 78. Detailed Structure of Periderm of *Canella alba*. Phelloderm developed as Stone-cells.

In the majority of cases the phellogen arises in the outermost region of the cortex, usually in the layer of cells immediately below the epidermis (the hypodermis), e.g. elder (Fig. 77, B). More rarely it may arise in the epidermis itself, as in *Solanum Dulcamara* (Fig. 77, A), or it may be deep-seated in origin, as in *Ribes* species, where it is formed in the pericycle (Fig. 77, C).

By repeated division of the phellogen, cells are formed to the exterior, and sometimes to the interior. The external cells form the tissue which we know as **cork.** They usually retain the rectangular shape and regular arrangement of the phellogen cells as seen in transverse section, but in surface view they appear somewhat polygonal in shape. As the cork cells mature, their walls become **suberised** and they lose their living contents. There are no intercellular spaces. The cork layer is therefore a dead, impermeable, insulating zone of tissue, and any living cells outside it are cut off from the vascular tissue and also die.

If cells are formed by the phellogen to the inside of it, as usually occurs where the phellogen is deep-seated in origin, they tend to lose their regular arrangement. They become normal parenchymatous, collenchymatous, or even sclerenchymatous cells and the tissue is called **phelloderm** (Fig. 78).

It is usual to refer to the phellogen, cork and phelloderm together as the **periderm.**

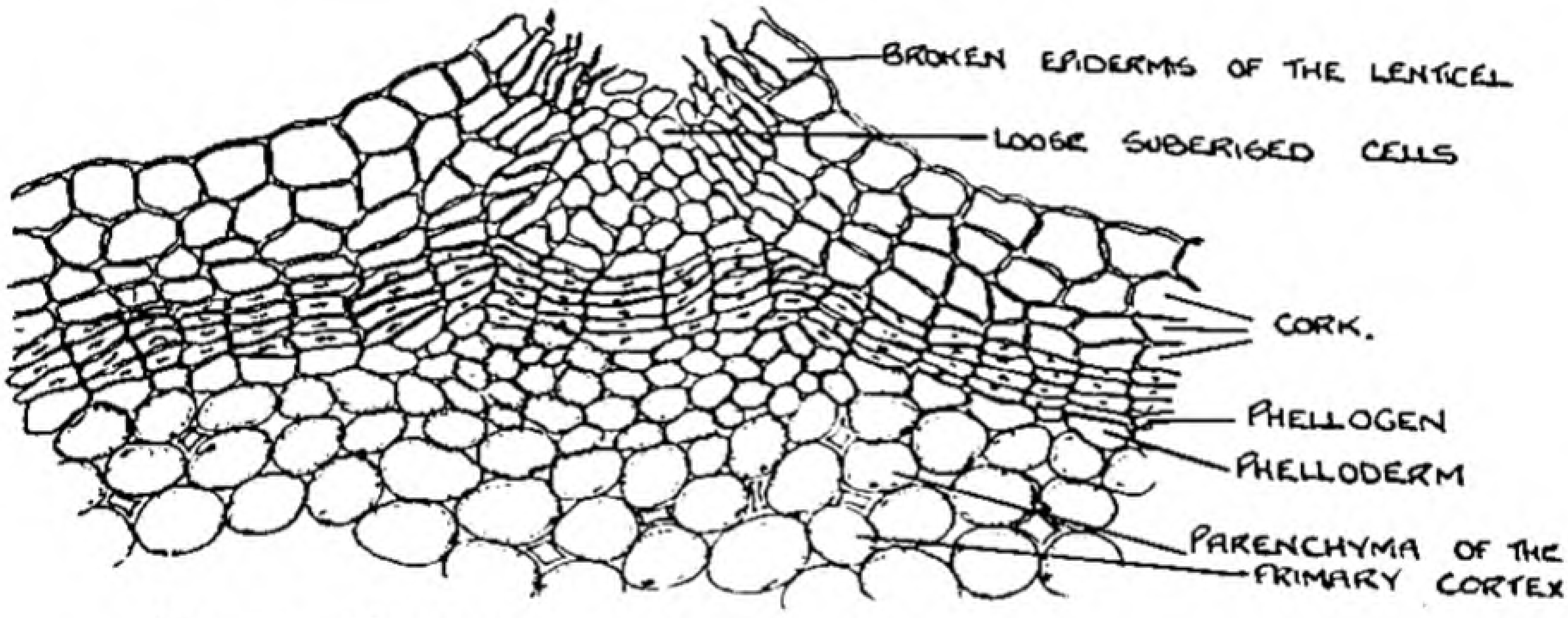

BROKEN EPIDERMIS OF THE LENTICEL
LOOSE SUBERISED CELLS
CORK.
PHELLOGEN
PHELLODERM
PARENCHYMA OF THE PRIMARY CORTEX

Fig. 79. DETAILED STRUCTURE OF LENTICEL OF *Sambucus*.
(As seen in T.S. Stem.)

A naked-eye examination of the surface of the cork covering a young stem shows that it is not uniform. Slits are present, which may be somewhat rounded and crater-like, or elongated either transversely or longitudinally. Seen under a hand lens they appear to be filled with a brown powdery substance. These structures are called **lenticels.** They are not accidental, but are formed by the phellogen and permit interchange of gases through the otherwise impermeable cork layer. It is possible to trace their development by examining sections under the microscope. They usually arise below the stomata of the original epidermis. The phellogen of the lenticel is cut off in the loose parenchymatous cells below a stoma. It proceeds to divide, and the cells formed external to it, unlike the cork-cells just described, round off whilst becoming suberised, leaving intercellular spaces (Fig. 79). These spaces form an intricate system through which slow gaseous diffusion can take place. Any phelloderm which may be produced internal to the lenticel phellogen, remains parenchymatous. Therefore, air containing oxygen may enter the stem and penetrate by slow diffusion through the intercellular spaces to all the living cells, making use of the medullary rays to reach the xylem parenchyma and pith. Similarly the carbon dioxide resulting from respiration, and water vapour, will diffuse outwards into the atmosphere.

In most woody plants the first-formed phellogen sooner or later ceases to function. In a few cases, notably in the cork-oak (*Quercus suber*), the same phellogen continues to produce cork year after year. In so doing it shows seasonal activity, like the xylem, and the smooth transverse surface of a bottle cork shows alternating zones corresponding to annual rings.

The cork-oak becomes productive of commercially useful cork from about thirty years old upwards. At about twenty years the first cork layer is stripped. The stripping induces a second phellogen to form below the original one. The virgin cork is of little commercial value, but after about ten years the second layer of cork is of good quality. Further strippings occur periodically, and the quality of the resulting new cork layers improves. Bottle corks are cut from these sheets of cork in such a way that the lenticels run transversely. The reason for this is obvious. For barrels of liquids which ferment and produce carbon dioxide, cork bungs are cut with the lenticels running longitudinally. If the gas were not allowed to escape in this way, the barrels might burst.

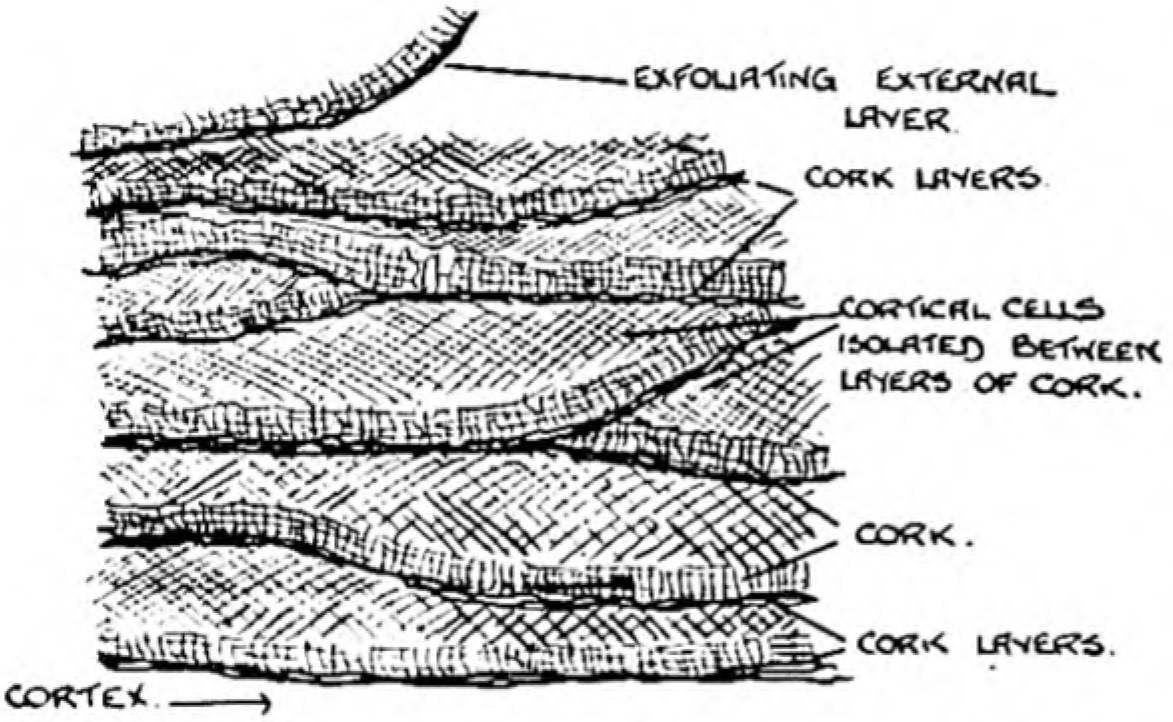

EXFOLIATING EXTERNAL LAYER
CORK LAYERS
CORTICAL CELLS ISOLATED BETWEEN LAYERS OF CORK.
CORK.
CORK LAYERS.
CORTEX

Fig. 80. STRUCTURE OF RHYTIDOME OF *Quercus Robur* (Diagrammatic).

In the majority of plants, when the first phellogen ceases to function, a second one has already formed in the tissues below it. This is succeeded by a third and a fourth, and so on. New cork layers successively formed from these may ultimately extend into the secondary phloem. Between these cork layers, patches of cells may be isolated, and die, together with the earlier-formed phellogens and their products, because of being cut off from their sources of supply. Such a composite periderm is called a **rhytidome** (Fig. 80).

The successive phellogen layers may be more or less continuous cylinders concentric with the peripheral layer, as in *Vitis* (grape-vine) and *Prunus* (cherry). This condition is known as ringed bark. More usually, the successively deeper phellogens are circumscribed plates which connect up on their margins with other similar plates, all of which produce layers of cork externally. On the surface of the trunk these layers appear as scales, and as the girth of the trunk increases, irregular cracks and fissures appear, widen and extend more and more deeply into the rhytidome. Such a periderm is commonly known as a scale bark.

Natural exfoliation, or peeling of the outer periderm in thin sheets, is familiar in birch (*Betula*), and regular shedding of the outer bark every spring in plane (*Platanus*). This is due to a regular alternation of thickened with unthickened layers in the cork, as a result of the activity of the phellogen. Either relatively thin-walled cork cells alternate with thick-walled lignified (stone) cells, or, thick-walled, suberised cork cells alternate with thin-walled unsuberised cells. In either case the thin-walled layers act as absciss layers.

29. Bark

The term "bark" is variously applied by different authorities. In the strict botanical sense the term is often restricted to the cork and other dead tissue to the outside of the functioning phellogen. On the other hand, in medicine, the term applies to all the tissues outside the cambium, and so includes the phloem. This is also true of the term as used popularly, for when we "bark" a tree the splitting takes place at the cambium. In view of the confusion it is advisable to retain the term bark only in its popular sense, and to use the terms periderm, cortex, phloem, etc., for more exact reference.

Apart from the suberised cell-walls, cork cells usually contain air, but in some cases yellow or brown contents may fill the cell cavities, and these may give the reaction for tannin, or the closely related phlobaphenes. Calcium oxalate may be present as raphides or druses. Granules of betulin give the characteristic white colour to birch bark.

The bark of the oak (*Quercus Robur*) is highly valued for tanning. The greater proportion of the tannin is present in the phloem region (inner bark). Cinchona bark contains quinine and other alkaloids, which appear to be present in the parenchyma. The cinnamon bark of commerce has had the cork layer removed by scraping and consists of the dried, inner cortex and phloem. The volatile oil which imparts the fragrant odour and sweet aromatic taste is present in special secretion cells found in the phloem. Slippery elm bark consists entirely of secondary phloem which contains large mucilage cells, as well as tangential bands of sclerenchymatous fibres.

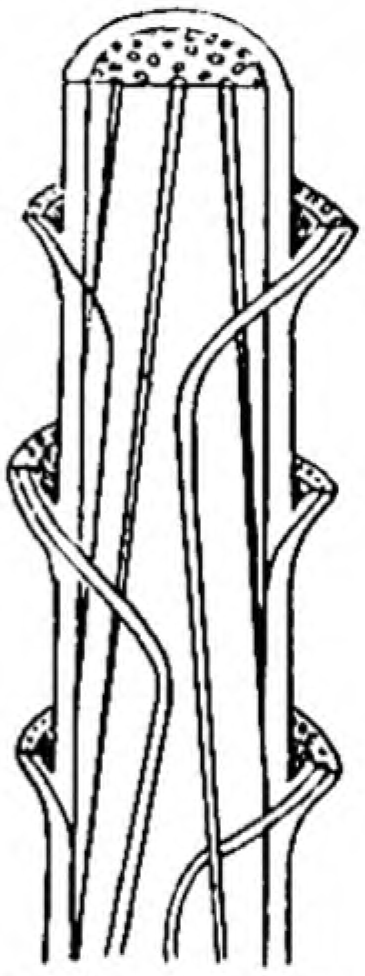


Fig. 81. DIAGRAM ILLUSTRATING COURSE OF VASCULAR BUNDLES IN THE STEM OF PALM-TYPE.

II.—THE MONOCOTYLEDON

30. The Arrangement

The arrangement of the vascular bundles in a monocotyledonous stem is usually described as scattered, but this is not always the case, as in the stolons of grasses, sedges, rushes, and indeed in many erect stems. Generally speaking it is true that monocotyledonous vascular bundles have no apparent regular arrangement. This is due to the behaviour of the leaf-trace bundles which enter the stem, usually from the sheathing leaf bases, and penetrate for varying distances towards the centre (Fig. 81). They then curve outwards and ultimately coalesce with other bundles near the periphery. Meanwhile they have remained independent through a varying number of internodes. Such bundles are referred to as *common bundles* because they are common to both leaf and stem. In addition there may be present *cauline bundles* which pertain to the stem, and *foliar bundles* which join on to other bundles immediately on entering the stem. The rest of the tissue within the epidermis may consist of an undifferentiated ground tissue of parenchyma, storing starch and other food reserves. Strengthening tissue may be present in the form of sclerenchyma, variously arranged, sometimes in bundles just below the epidermis, sometimes in larger masses in which the outer vascular bundles are embedded, sometimes forming a sheath round the individual bundles. In some stems, particularly stolons and rhizomes, a central cylinder of ground tissue, in which are numerous vascular bundles, is separated from an outer parenchymatous cortex by an endodermis in which the cells have suberised walls.

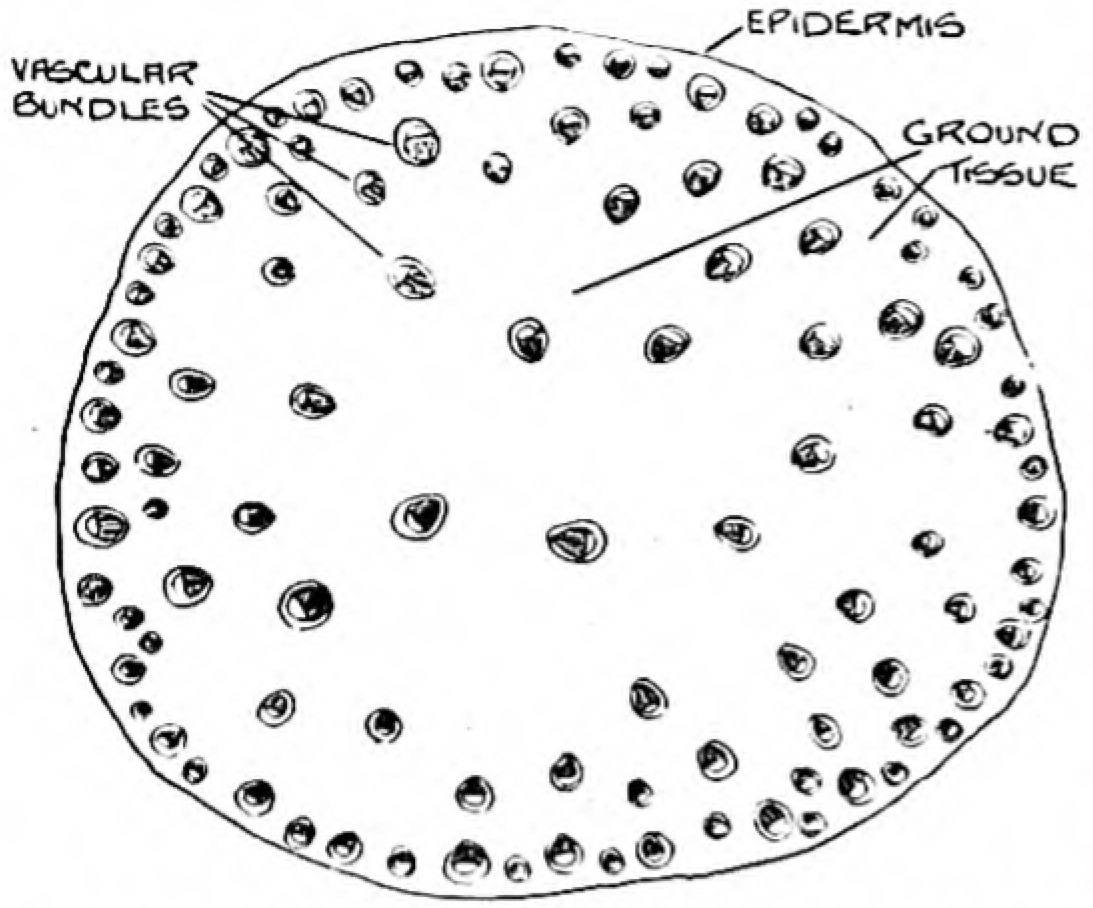


Fig. 82, A. MAIZE-STEM, TRANSVERSE SECTION, DIAGRAM.

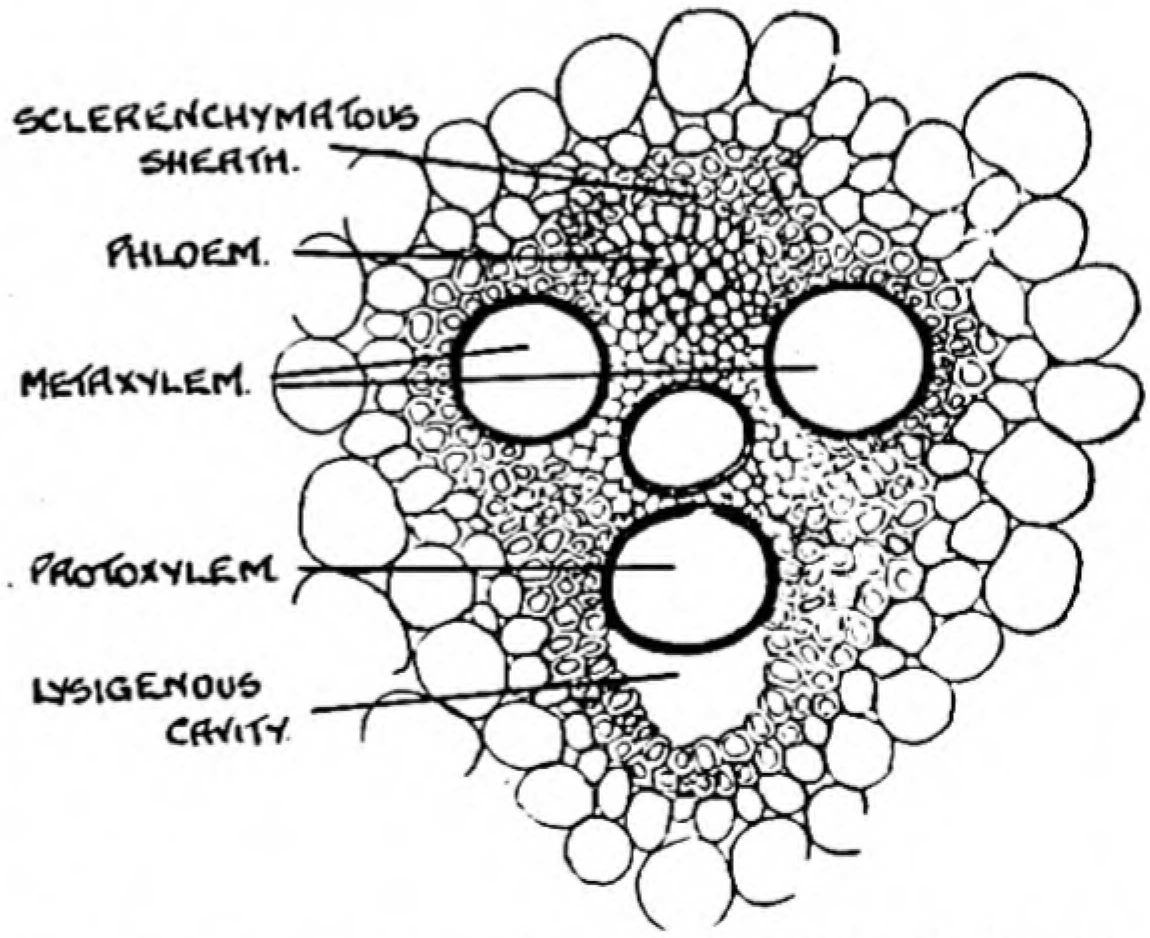


Fig. 82, B. DETAIL OF A VASCULAR BUNDLE.

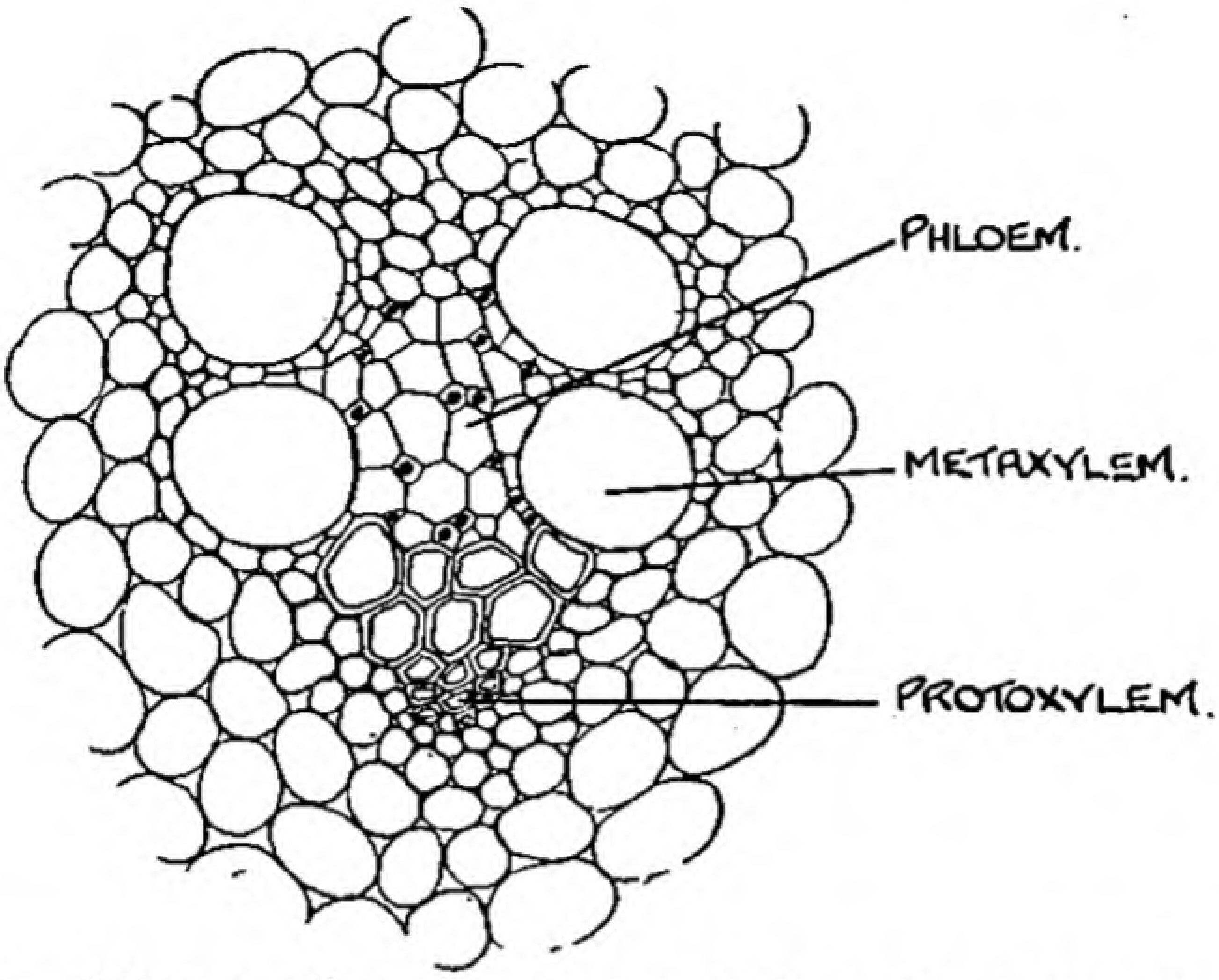


Fig. 83. *Asparagus* STEM, DETAILED T.S. OF VASCULAR BUNDLE.

31. The Vascular Bundle

If we take the stem of maize (Fig. 82) as an example of a monocotyledonous stem we find numerous bundles scattered throughout a ground tissue which is undifferentiated into cortex and central cylinder. Each bundle is more or less enclosed in a sheath of sclerenchymatous fibres, and is collateral. The metaxylem consists of two large pitted vessels connected by tracheides. Internal to these is the protoxylem consisting of spiral and annular vessels

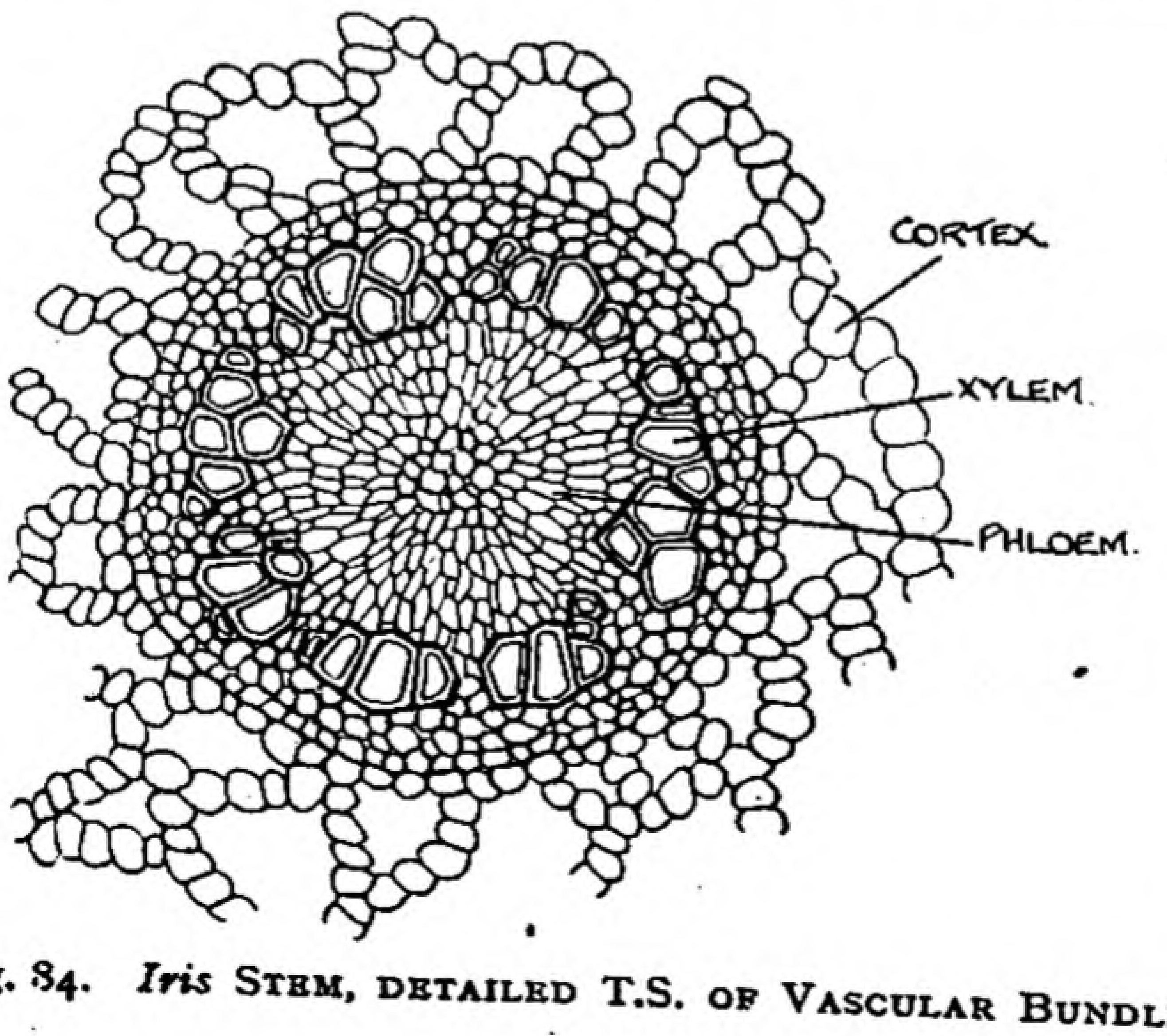


Fig. 84. *Iris* STEM, DETAILED T.S. OF VASCULAR BUNDLE.

associated with thin-walled xylem parenchyma. The innermost protoxylem elements, the annular vessels, may have been broken down, leaving a lysigenous cavity. External to the tracheides is the phloem, in which can be distinguished larger, apparently empty sieve-tubes, and smaller companion cells filled with contents. There is no cambium; on this account the bundles are described as *closed*. This is an important distinction from the dicotyledonous vascular bundle.

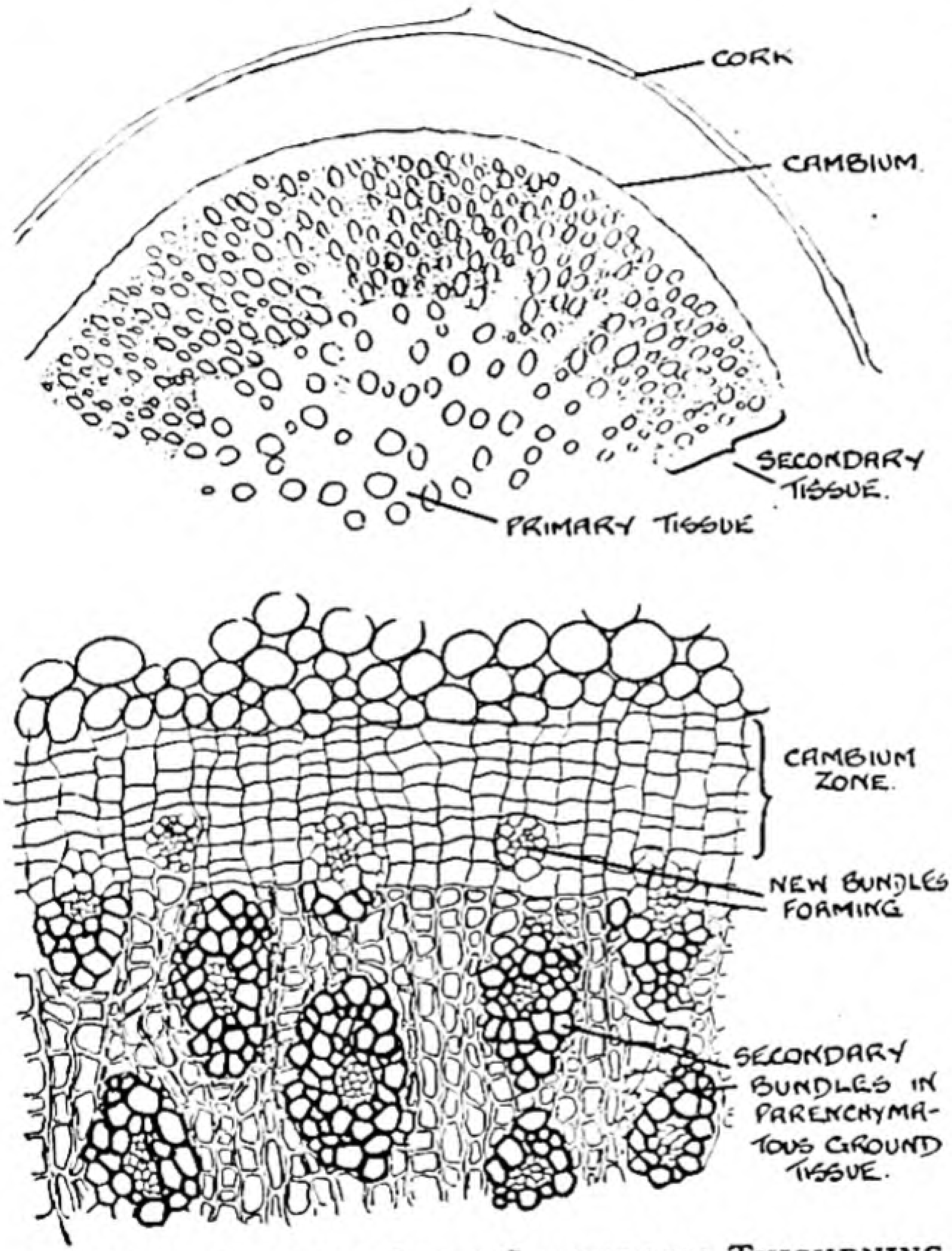


Fig. 85. *Dracaena* Stem, Secondary Thickening.

32. Modifications

In some monocotyledonous stems, e.g. *Asparagus* (Fig. 83), the xylem is in the form of a **V**, with the point occupied by protoxylem and the arms the metaxylem with vessels of increasing diameter. The phloem lies between the arms of the **V**. In other stems, e.g. *Iris* and *Acorus Calamus* (sweet flag) rhizomes, the xylem may even encircle the phloem (Fig. 84). In grasses, bundles of the maize type are arranged in more or less concentric rings, often associated with sclerenchyma, round a central cavity. In the leafy stems of *Tamus* (black bryony) the vascular bundles are arranged in a ring surrounding a pith, as in Dicotyledons.

Some Monocotyledons, such as *Dracaena, Yucca*, the screw pines and the palms attain tree-like dimensions. In the palms the whole of the tissues of the stout stem are derived from a massive apical meristem. This gives rise to a parenchymatous ground-tissue containing numerous, scattered, closed vascular bundles. No cambium develops and therefore there is no secondary thickening.

Dracaena, Yucca and a few others possess a form of secondary growth. In *Dracaena*, for example, the primary condition of the stem shows the scattered arrangement of closed, common bundles. A secondary meristem originates in the ground tissue outside the outermost leaf-trace bundles. This cambium cuts off cells internally and externally. The tissue produced internally differentiates into vascular bundles, separated by parenchyma which may become lignified and pitted, or remain thin-walled (Fig. 85). The secondary vascular bundles consist of a little phloem surrounded by xylem formed of tracheides. The small amount of secondary tissue external to the cambium is thin-walled parenchyma.

Periderm may be present in Monocotyledons, but it rarely shows the regular arrangement seen in Dicotyledons. The epidermis is usually replaced by primary cortical cells becoming suberised. But in a few instances (*Dracaena, Yucca, Zingiber*, etc.) such suberised cells may be associated with groups of periderm to form a rhytidome.

III.—GENERAL

33. Origin of Lateral Branches

In both Dicotyledons and Monocotyledons axillary buds have a superficial origin from the apical meristem of the parent-stem. They arise as little protuberances of dermatogen and periblem only (Fig. 32). The plerome of the parent-axis takes no part in their formation. For this reason their development is said to be **exogenous.** As the axillary protuberance increases in size a plerome (derived from the periblem of the parent axis) differentiates, and becomes connected with the plerome of the parent. Young leaves begin to grow out and overlap the apex. Thus we have an axillary bud which in all respects reproduces the structure of the apical bud of the parent-axis.

34. Healing Wounds

When a stem or other part of the plant is injured the wound as a rule soon heals. Immediately after the wounding the uninjured cells in the neighbourhood of the wound are stimulated to form a secondary cork cambium, which produces a layer of cork so that the wounded surface is soon isolated by an impermeable layer from the inner living and uninjured tissues. This type of healing is readily seen in a potato-tuber that has been damaged. Both Monocotyledons and Dicotyledons possess this capacity of healing.

In woody plants, if a branch is cut across, the uninjured living cells (generally the cambium) adjacent to the wounded surface produce a mass of undifferentiated parenchymatous tissue called a callus, and this may later develop on or near its surface a layer of cork. If the cambium is injured the two cambial surfaces both produce callus tissue so that any gap between them is bridged. In this bridge of callus a new cambium arises. The continuity of the cambium is thus achieved and provision is made for the continued formation of secondary tissue. This is the basis of the practice of grafting in which the cut surfaces of two shoots (the stock and the scion) are brought into contact and protected against desiccation so that they each form callus and unite. For such a union to take place the two shoots must be of the same or of closely related species.

35. Knots (Fig. 86)

As the successive annual rings of xylem are added to the woody cylinder, the bases of existing branches will become more and more embedded in it. When a living branch is cut off, or broken off, the wounded surface becomes covered by a layer of callus, and if the tree goes on increasing in thickness the layers of secondary wood will gradually encroach over the stump of the branch which thus becomes embedded in newer wood. Meanwhile the living tissues of the stump may have died and shrunk, leaving a loose cone of wood belonging to the stump embedded in the wood of the trunk. When the tree is converted to timber the branch bases are disclosed as knots. Often the lower branches of the tree die naturally, and may be broken off, but their basal portions persist and become surrounded by the later formed secondary wood, forming knots. If, therefore, the lower branches of a tree are removed at an early age, the secondary wood formed early in the life of the tree, *i.e.* in the central part of the trunk, may contain knots, but the outer region of the secondary wood will be free from these inclusions.

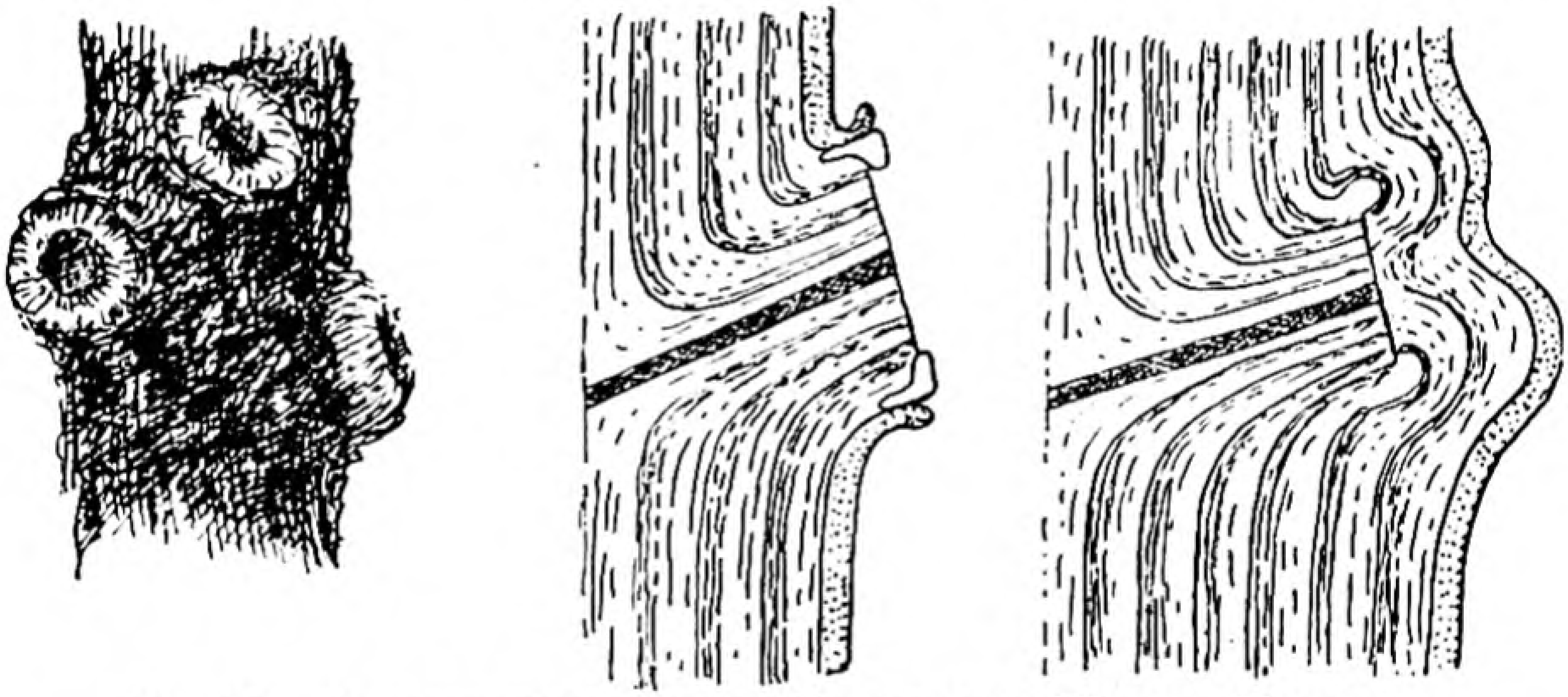


Fig. 86. ILLUSTRATING CALLUS FORMATION, WOUND HEALING, KNOT FORMATION IN WOOD.

CHAPTER V

THE ROOT OF THE ANGIOSPERM

1. General Characters

The root may be defined as that organ of a plant which tends to grow downwards, away from light and towards water; which, as a rule, bears neither leaves nor buds; and which usually has at the apex a protective cap of tissue called the **root-cap.** The internal structure and development, also, are characteristic. It is by consideration of these characters that true roots can be distinguished from root-like stems.

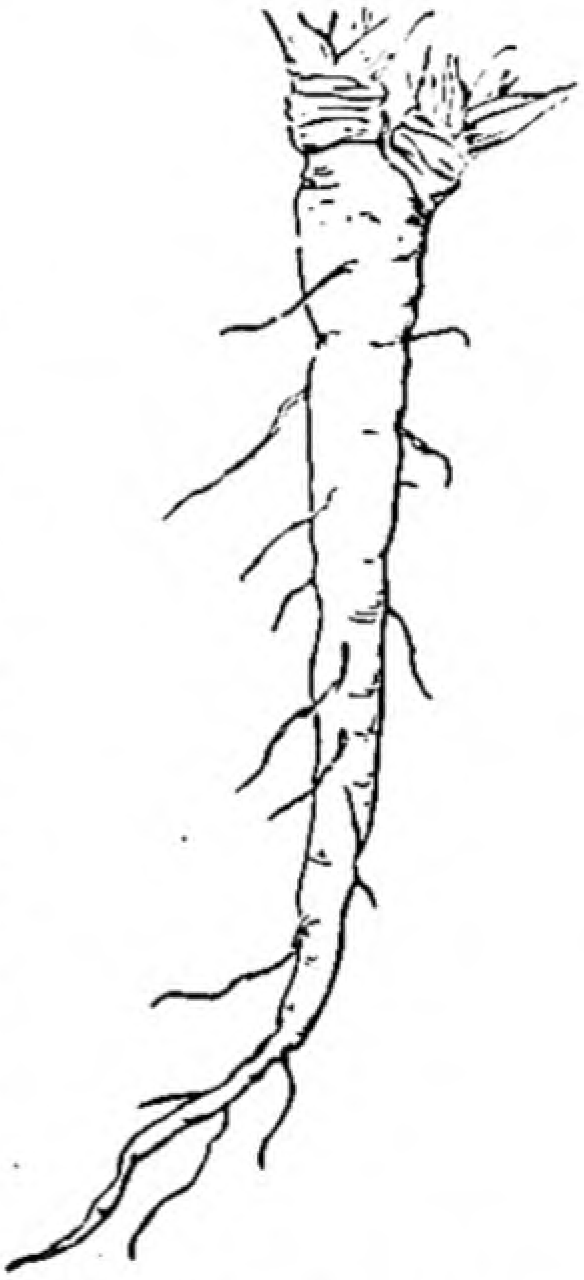


Fig. 87. TAP-ROOT OF *Taraxacum.*

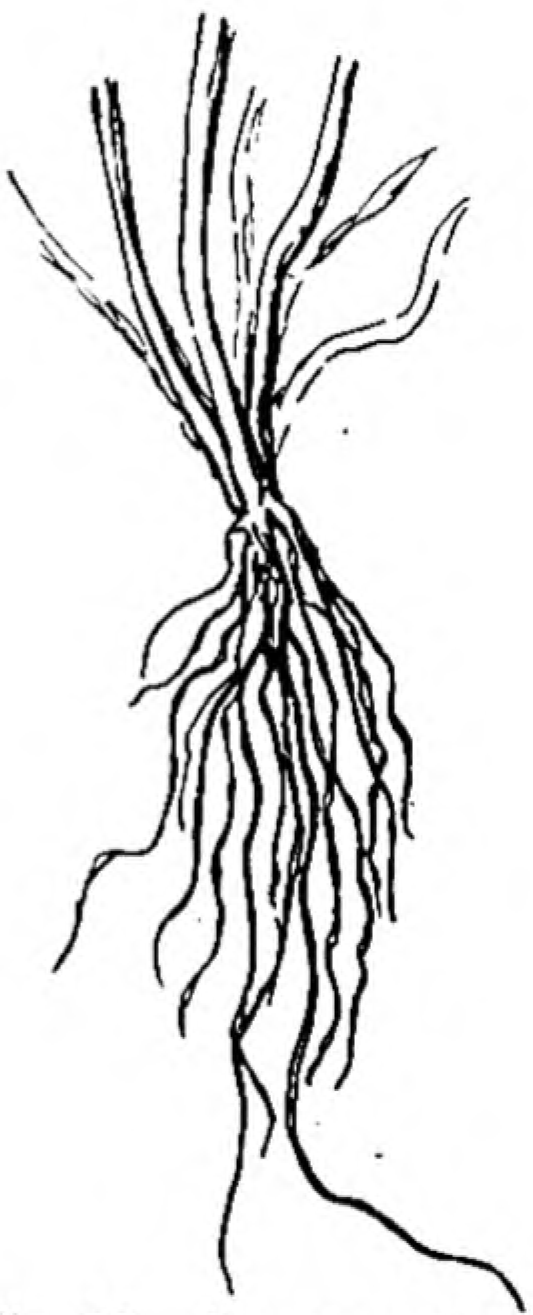


Fig. 88. FIBROUS ROOT OF GRASS.

A. EXTERNAL CHARACTERS

2. Tap and Adventitious Roots

As already explained, the radicle is the embryonic primary root. In the majority of *Dicotyledons* the radicle, at germination, elongates, grows down into the soil, branches, and forms the root-system of the plant. This is known as a *tap-root system*. The elongated primary root is described as a **tap-root,** and the branches, if developed in regular acropetal succession, as *normal secondary roots*. The branching is invariably lateral (Fig. 87).

In many Dicotyledons, more especially in those with rhizomes, runners, trailing stems, etc. (e.g. Figs. 52 and 53), and in the majority of Monocotyledons we may have **adventitious roots** (Fig. 88). These are roots developed (*a*) on stems; (*b*) in a few cases on leaves.

3. Forms and Functions of Roots

Roots are usually buried in the soil and hence exist in a much more uniform environment than stems. Only where they are exposed to light do they develop chlorophyll. Normally, when young, they are white in colour, becoming brown with age. The root fixes the plant in the soil and absorbs from the soil, water and mineral substances. Sometimes, however, roots function also as storage organs or are specialised to form climbing organs, or spines, and they may even grow up out of the ground to form "breathing roots."

A common form of root, especially amongst herbaceous Dicotyledons is the tap-root. Here the primary or main root continues to grow as long as the plant lives, and may penetrate the soil to considerable depths. Thus, the tap-root of sea holly (*Eryngium maritimum*), a plant of sand-dunes, may reach a depth of eight feet or more. Such roots do not branch freely. Other types remain short and stout, and send out an extensive system of lateral branch roots. The former kind may be regarded as "deep-feeders," the latter as "surface-feeders."

Surface feeding is also afforded by the adventitious fibrous roots of some Dicotyledons and the majority of Monocotyledons. Such roots arise from underground stems, and, like those of annual plants, are thin, with no great reserve of food-material.

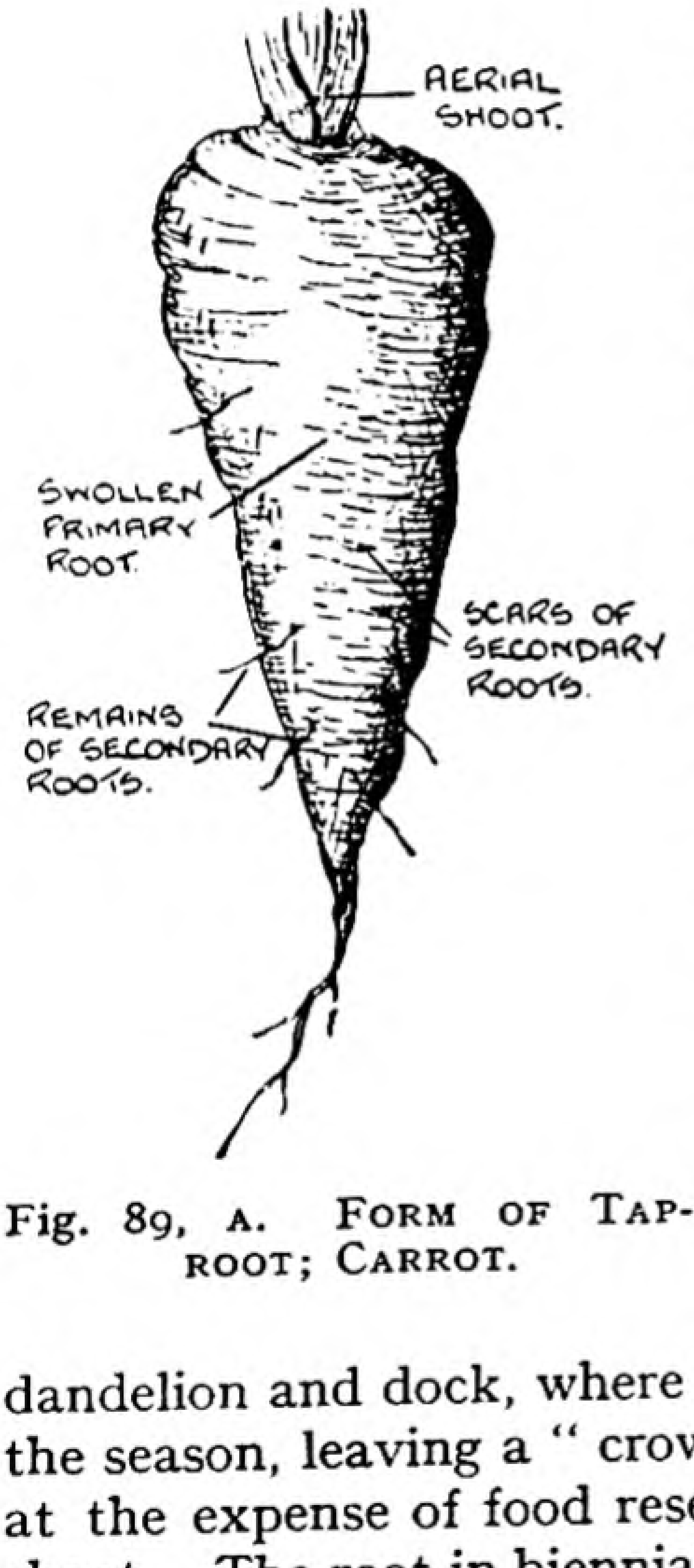

AERIAL SHOOT.
SWOLLEN PRIMARY ROOT.
SCARS OF SECONDARY ROOTS.
REMAINS OF SECONDARY ROOTS.

Fig. 89, A. FORM OF TAP-ROOT; CARROT.

4. Forms of Tap-roots (Fig. 89, A)

The roots of perennial plants, on the other hand, contain reserve food-materials which will sustain growth in the early part of the following year. They may be thick and fleshy as in dandelion and dock, where the aerial parts die down at the end of the season, leaving a "crown" of buds which grow up next season at the expense of food reserves in the fleshy roots and base of the shoot. The root in biennial plants, too, may become swollen during the first year of growth, and many such swollen roots are utilised as vegetables, e.g. carrot, parsnip, salsafy, scorzonera and beet-root. The food-value of these roots depends on the stored food material that they contain, and this is generally a carbohydrate. If left in the ground for a second year, such roots give up their food material to the buds at their "crown." These develop flowering shoots and set seed, when the entire plant dies. The first year's growth of biennials is usually entirely vegetative.

5. Forms of Adventitious Roots

Adventitious roots frequently become tuberous, also, owing to storage of food-materials. Examples are seen in *Dahlia*, *Ipomoea*, *Aconitum*, *Ranunculus Ficaria* and many terrestrial orchids. These root-tubers may be simple and undivided, or double, *i.e.* branched into two; or branched in a finger-like manner. They arise in relation to axillary buds, usually one to each bud, near ground level. The surplus food-material from the aerial shoot passes down into each developing root-tuber, causing it to swell. In aconite (*Aconitum Napellus*) it is mainly the secondary phloem which acts as the storage tissue; in lesser celandine (*Ranunculus Ficaria*) it is the cortex; in both, the storage cells are packed with starch grains. In *Dahlia* the food-reserve is inulin. Towards autumn the parent plant dies down, and each root-tuber, with bud attached, remains in the soil to propagate the plant next season. The root-tubers of *Ipomoea purga*, known as jalap, are swollen adventitious roots formed at the nodes of slender underground stems. The tuberous roots of *I. Batatas* (sweet potato) are used like potatoes.

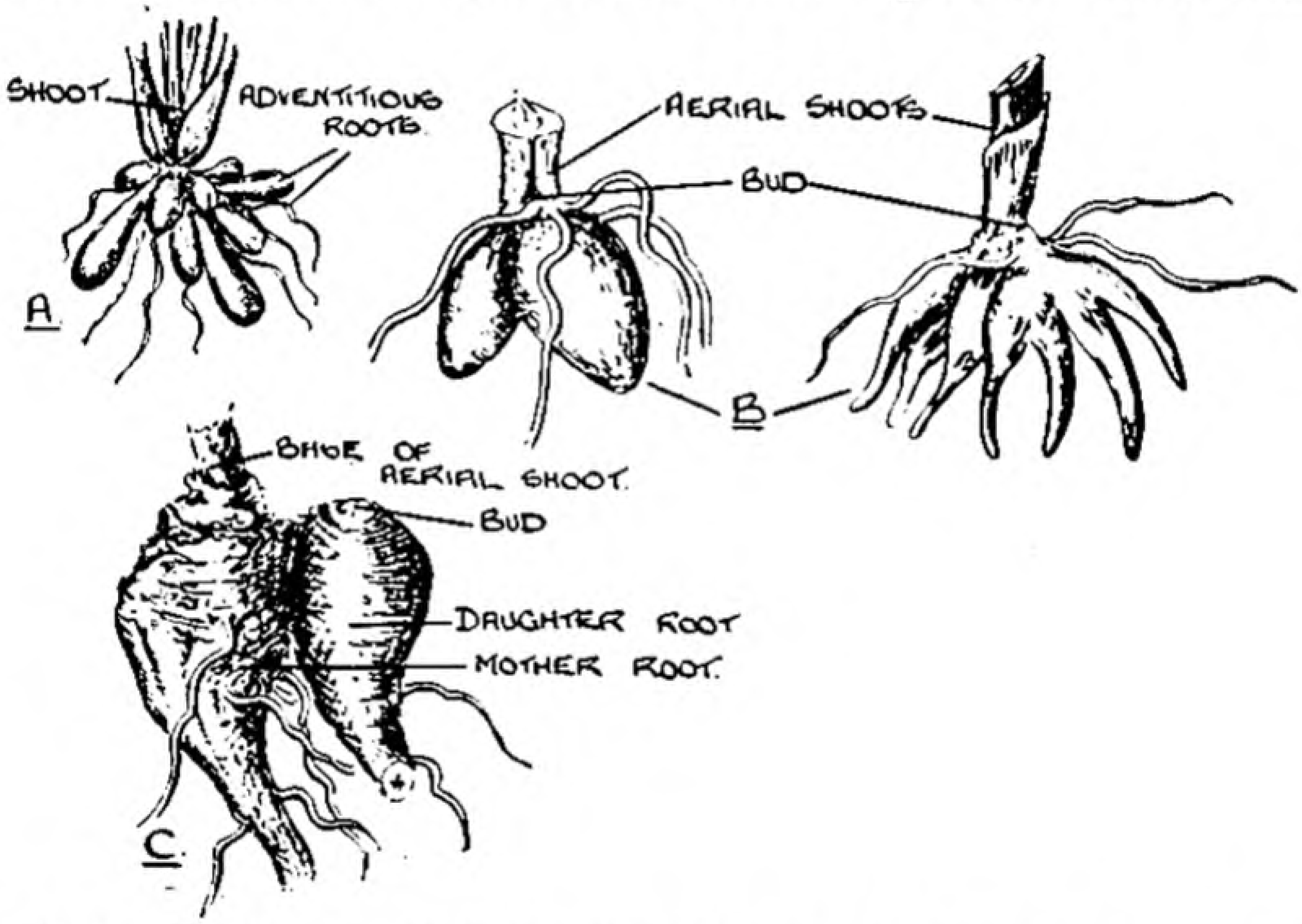


Fig. 89, B. FORMS OF ADVENTITIOUS ROOTS; A, *Ranunculus Ficaria*; B, *Orchis*; C, *Aconitum*.

Sometimes adventitious roots are aerial, as in many orchids, where they absorb moisture from the air (Fig. 120). Occasionally aerial roots function as climbing organs, as in *Ficus repens*. Many parasitic plants have absorbing organs, generally called haustoria, which may represent specialised roots, although their exact morphological nature is not always clear (Fig. 149). Certain members of the Scrophulariaceae are semiparasites, in that their roots attach themselves to the roots of other plants from which they draw water and mineral salts, but their aerial portions are green and can photosynthesise carbohydrates. The primary attachment to the root of the host is by means of an organ which may be radicle or hypocotyl; secondary attachments are effected by means of adventitious roots. Breathing roots, which may or may not be adventitious, occur especially in some tropical swamp plants (e.g. mangroves), the normal roots of which live in an environment extremely poor in oxygen, and the breathing roots grow up into the air. Through these roots, oxygen is able to diffuse to the tissues of the submerged parts of the plant. In some Orchidaceae and in Podostemonaceae roots may possess chlorophyll and be photosynthetic organs. A few plants possess root spines or thorns, e.g. *Pothos armatus* and *Acanthoriza*.

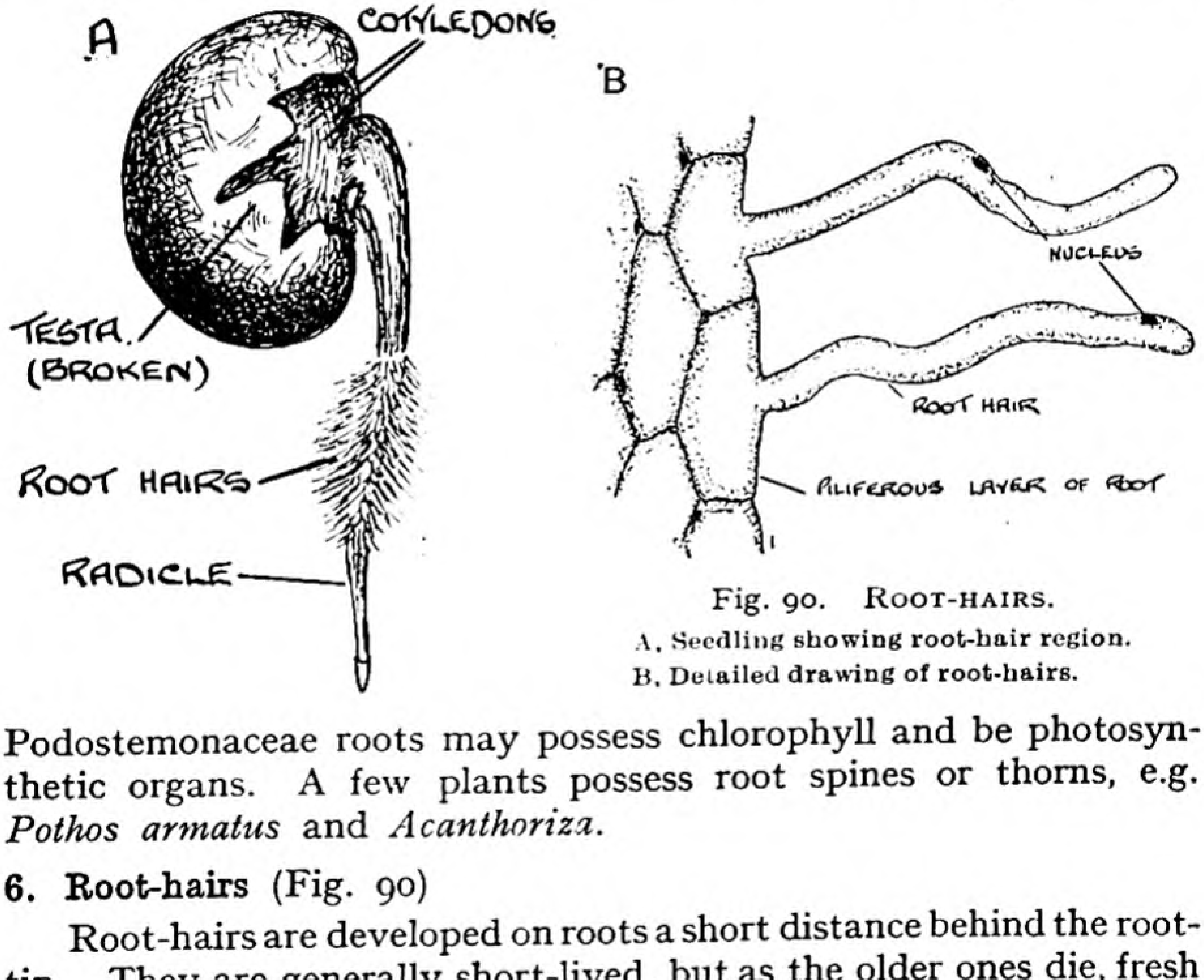


Fig. 90. ROOT-HAIRS.
A, Seedling showing root-hair region.
B, Detailed drawing of root-hairs.

6. Root-hairs (Fig. 90)

Root-hairs are developed on roots a short distance behind the root-tip. They are generally short-lived, but as the older ones die, fresh ones are continually being produced near the apex as long as it is actively growing. The absorption of water and mineral salts from the soil is effected by them and their development is encouraged by an abundant supply of air. They may be readily observed on roots that are growing in saturated air—conditions which obtain in the spaces between the soil particles in moist well-aerated soil. If young seedlings are carefully lifted from such soil, soil particles will be seen firmly adhering to the root-hairs. On account of their delicate nature the root-hairs are easily injured. Lack of oxygen may inhibit the development of root-hairs, and they are frequently absent from the roots of water plants.

B. INTERNAL STRUCTURE

7. The Apical Region

We have already noticed (p. 35) that, in sections of the apical meristematic region of the root, it is often possible to recognise four histogens. In this respect the root apex differs from that of the stem, which only has three, viz. dermatogen, periblem and plerome. The additional one in the root is the calyptrogen which gives rise to the root-cap. The calyptrogen may be a quite distinct layer at the apex, as in Monocotyledons such as the grasses, or it may originate in a layer in common with the dermatogen, and the root-cap cells arise by periclinal divisions from it (as in many Dicotyledons.) In either case the root-cap cells are pushed outward (forward) and form a protective covering to the delicate apical meristem as the root elongates and pushes its way through the soil. The cells at the extreme tip become loose, through changes in the cell-wall, and are removed by this process, but the meristem is continually producing more to replace them.

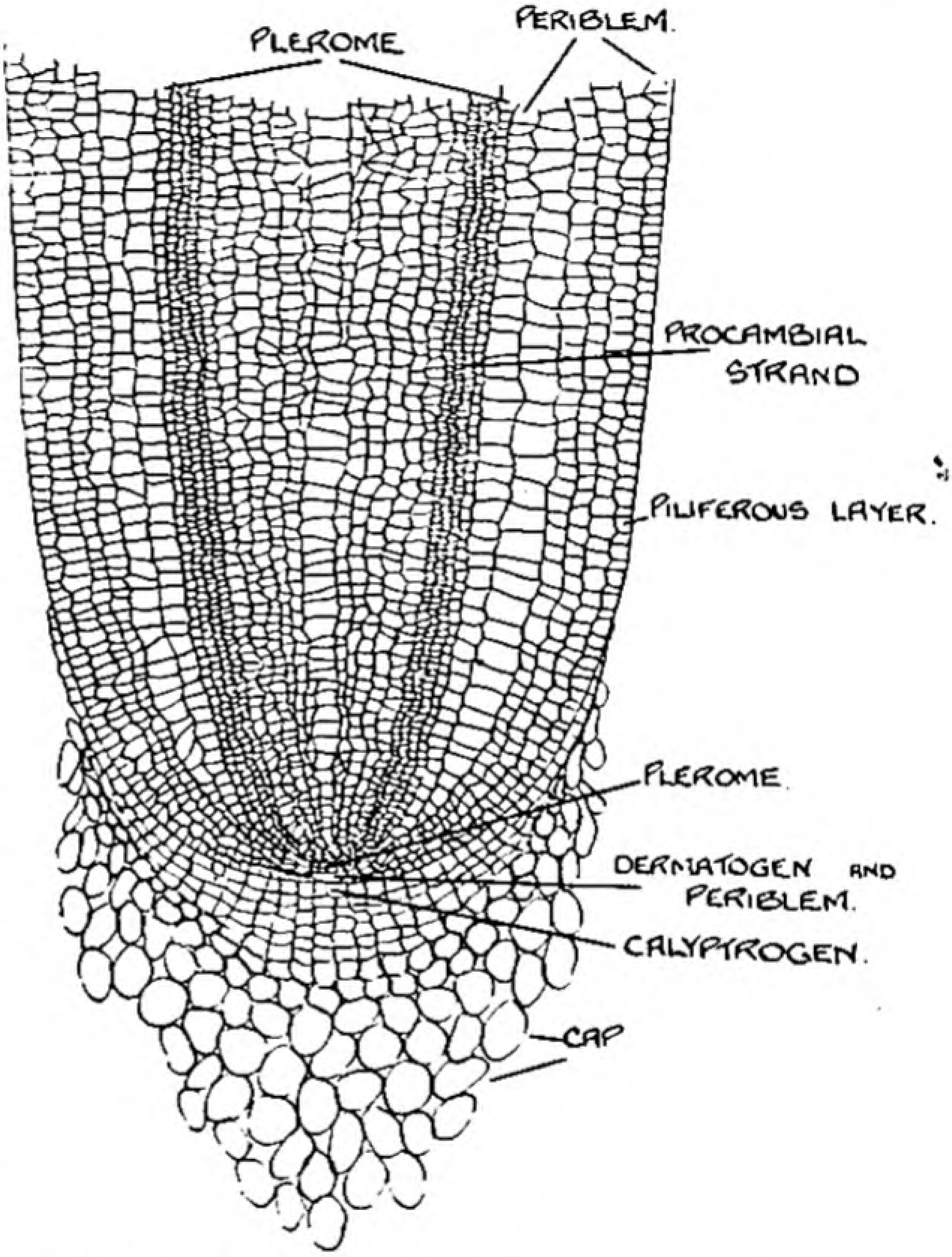


Fig. 91. ROOT APEX OF MONOCOTYLEDON.

The dermatogen gives rise to the piliferous layer of the root. This may persist, even after the root-hairs have withered, as a

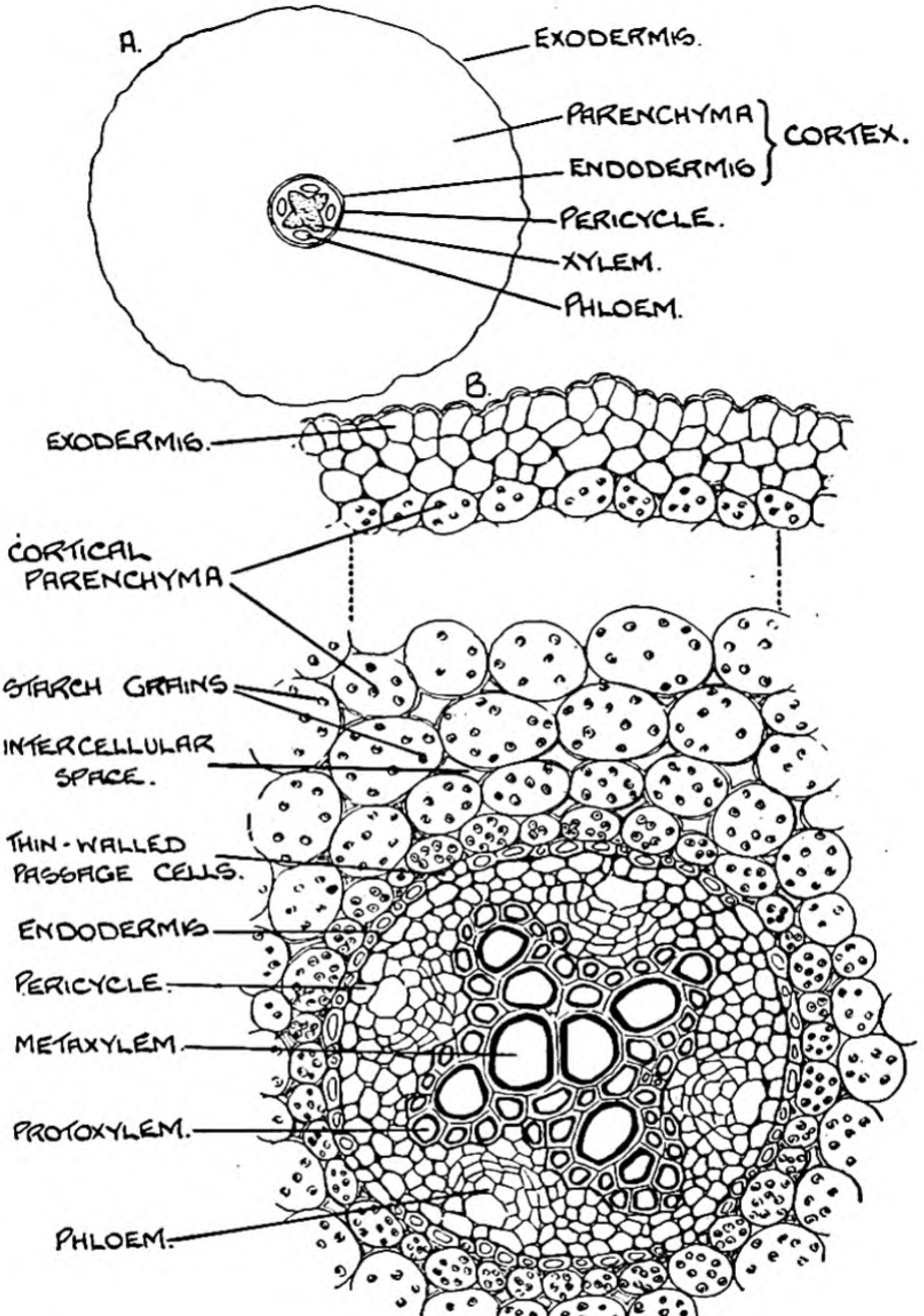

A.
EXODERMIS.
PARENCHYMA
ENDODERMIS
CORTEX.
PERICYCLE.
XYLEM.
PHLOEM.
B.
EXODERMIS.
CORTICAL PARENCHYMA
STARCH GRAINS
INTERCELLULAR SPACE.
THIN-WALLED PASSAGE CELLS.
ENDODERMIS
PERICYCLE.
METAXYLEM.
PROTOXYLEM.
PHLOEM.

Fig. 92. ROOT OF DICOTYLEDON (*Ranunculus repens*) IN TRANSVERSE SECTION.

A, Diagrammatic; B, Detail.

protective layer in roots which do not undergo secondary thickening. More usually, however, it disappears, and in such roots the hypodermis assumes the role of protection (see Fig. 92). The periblem, as in the stem, gives rise to the cortical ground-tissue. The plerome gives rise to the central cylinder or stele containing the vascular tissue with its associated conjunctive tissue. **Procambial** or desmogen **strands** make their appearance in it, and, on further development, these are *completely* differentiated into vascular tissue—some into xylem, others, alternating with them, into phloem. The differentiation of both xylem and phloem begins on the outer side of the procambial strands so that the protoxylem and protophloem both lie to the outside of the metaxylem and metaphloem respectively. This order of differentiation is described as centripetal, and the protoxylem and protophloem are said to be exarch.

8. Primary Structure of Roots (Figs. 92 and 93)

A transverse section of a monocotyledonous, or of a *young* dicotyledonous, root (Figs. 92 and 93) shows the vascular tissue more or less aggregated towards the centre. The xylem has a stellate arrangement. The protoxylem occupies the points of the "star"; the metaxylem is towards the centre. The **phloem bundles** are equal in number to, and alternate with, the protoxylem points, so that they are situated on different radii of the transverse section. The xylem and phloem are separated by *conjunctive tissue.*

In many roots all the xylem bundles fuse or meet in the centre of the root in a number of large pitted vessels; in this case there is no pith. In others, the centre of the root is occupied by a parenchymatous, sometimes sclerenchymatous, tissue, which may be called the pith.

In Dicotyledons the number of xylem rays terminating in protoxylem is generally much fewer than in Monocotyledons. The number in the former is usually from two to five, in the latter, twelve to twenty. According to the number of rays we describe the xylem as diarch, triarch, tetrarch, pentarch, etc., and polyarch.

The vascular cylinder is surrounded by two special layers of cells. The inner layer consists of parenchymatous cells with protoplasmic contents, and is the **pericycle.** It is the outermost layer of the stele. In the roots of Angiosperms it is usually a single layer but it may not be continuous, as in some roots the protoxylem abuts on the endodermis. The outer of the two layers is the **endodermis**, and is the innermost layer of cortical tissue developed from the periblem. Its cells in transverse section are four-sided, and slightly elongated tangentially. The radial walls have a suberised band or strip, called the Casparian strip after its discoverer. In a transverse section of the root this strip appears as a slight lenticular thickening on the radial walls of the endodermis, and can be stained with suitable stains. In dicotyledonous roots, as we trace the endodermis backwards, we find that cell walls become more uniformly thickened with either suberin or lignin.

In monocotyledonous roots the Casparian strip is visible only in the very young endodermis. Here the cells soon develop a further thickening of the radial and inner walls, described as **U**-shaped, but the endodermal cells opposite the protoxylem groups remain unthickened, and are called passage cells.

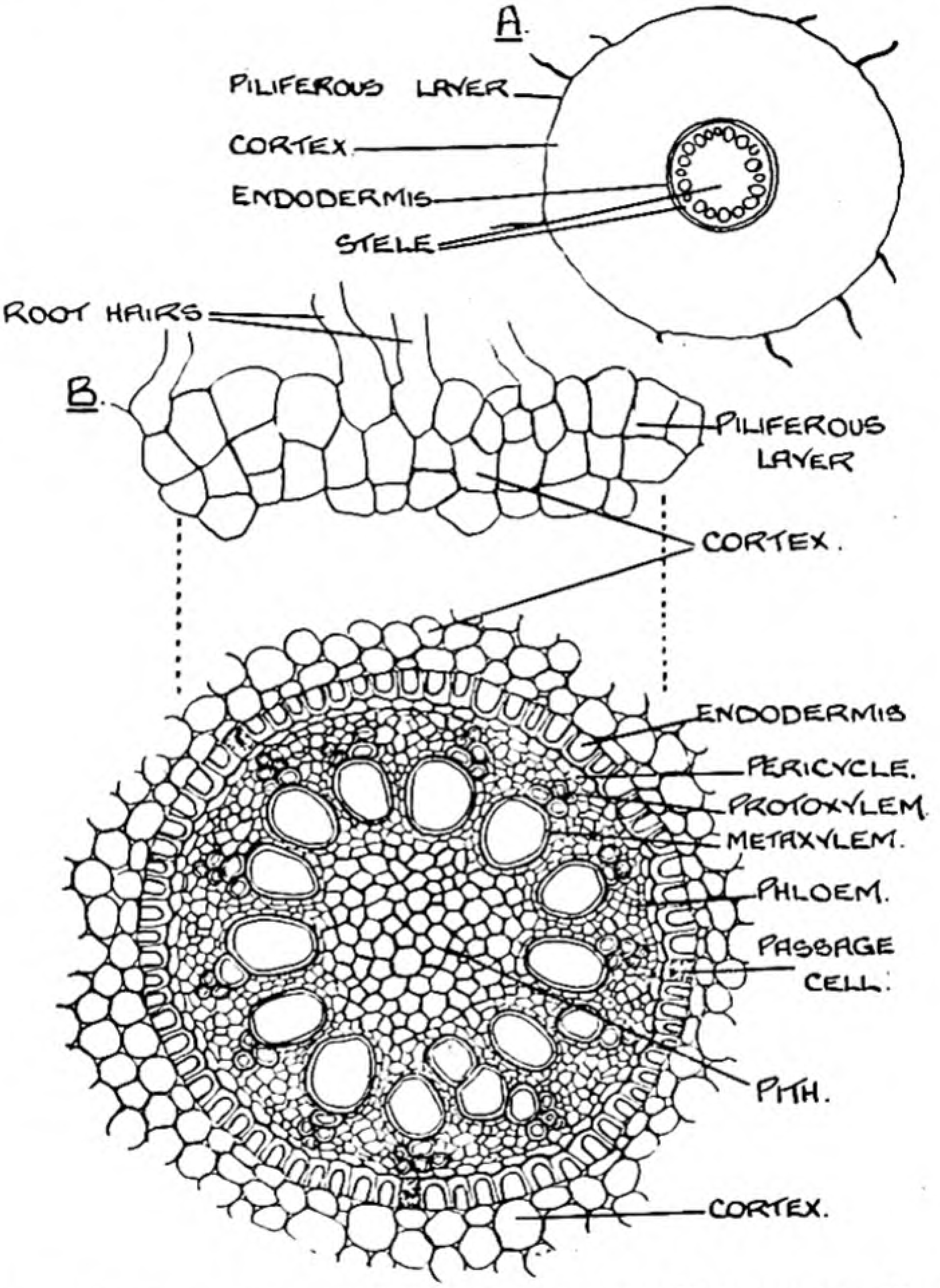

A.
PILIFEROUS LAYER
CORTEX
ENDODERMIS
STELE
ROOT HAIRS
B.
PILIFEROUS LAYER
CORTEX.
ENDODERMIS
PERICYCLE.
PROTOXYLEM.
METAXYLEM.
PHLOEM.
PASSAGE CELL.
PITH.
CORTEX.

Fig. 93. ROOT OF MONOCOTYLEDON (*Iris*) IN TRANSVERSE SECTION.
A, Diagram; B, Detail.

The absence of intercellular spaces prevents diffusion of air between cortex and central cylinder. The suberisation of the radial walls makes them more or less impermeable to water, and may prevent uncontrolled water movement between the vascular and cortical tissues. "Leaking" of water along the radial walls of the endodermal cells is practically prevented. Water can pass the endodermis only by passing across the constituent cells.

9. Secondary Growth in the Dicotyledon

In the roots of most Dicotyledons, a cambium, and later a phellogen, arise as secondary meristems, and secondary growth takes place. In Monocotyledons there is no secondary growth, and the same structure can be recognised in all the fully developed regions of the root.

When secondary growth is about to begin, certain cells lying on the inner side of each phloem bundle become meristematic (Fig. 94). Thus strips of **cambium**, equal in number to the phloem bundles, make their appearance. These gradually extend outwards between the xylem and phloem, *owing to more of the parenchymatous cells becoming meristematic.*

The curved strips of cambium thus produced come into contact with the pericycle on each side of the protoxylem. These pericycle cells now become meristematic, and, in this way, the cambium strips are united outside the protoxylem groups. Thus a continuous wavy band of cambium is formed, running internal to the phloem bundles, external to the xylem. It should be recognised that this cambium is entirely a secondary meristem, arising partly from parenchymatous cells between xylem and phloem, partly from the pericycle.

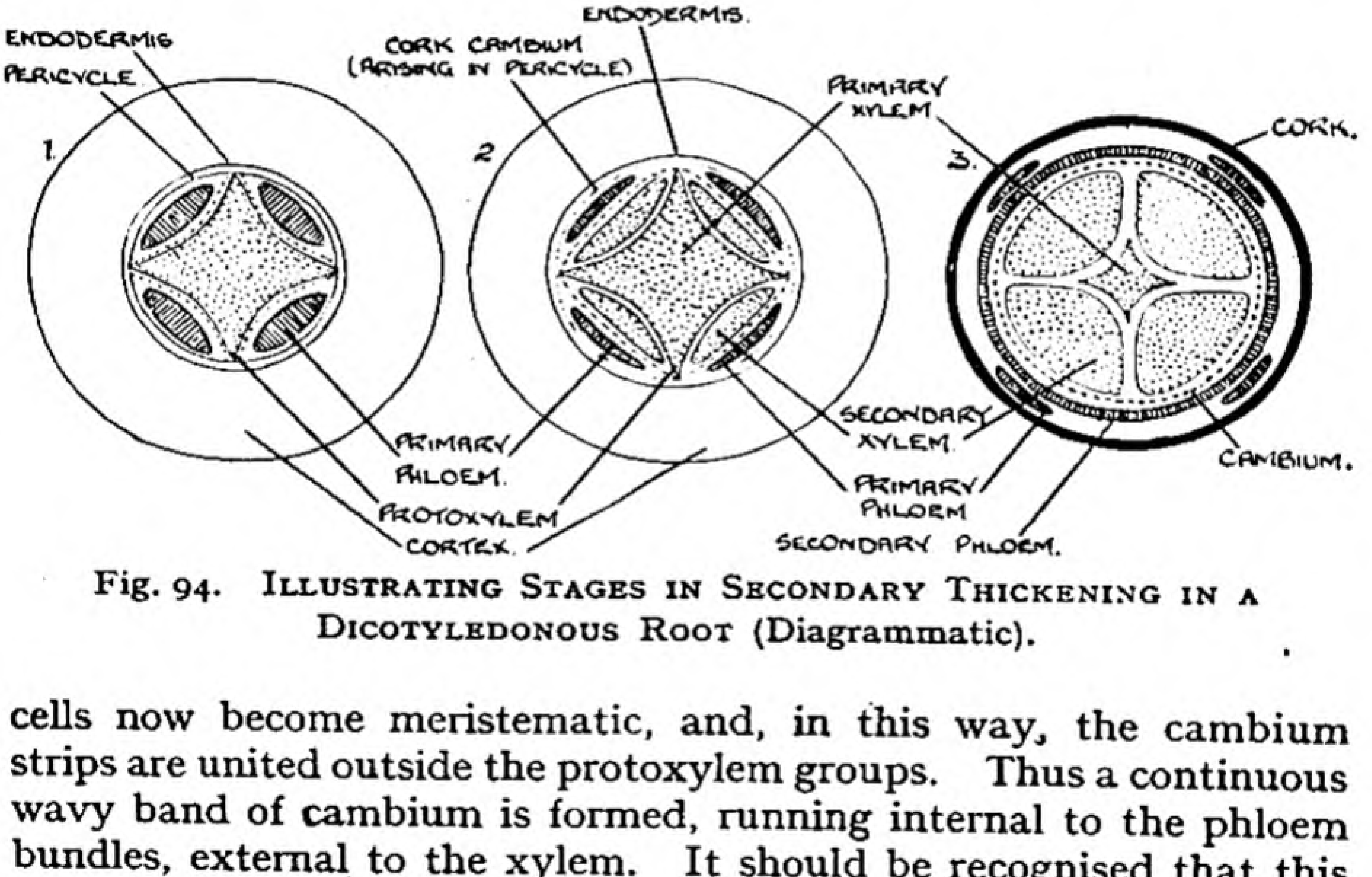


Fig. 94. Illustrating Stages in Secondary Thickening in a Dicotyledonous Root (Diagrammatic).

The cambium cells divide exactly as in the stem. The **secondary xylem** is laid down on its inner side. The **secondary phloem** is formed outside the cambium, and, together with the primary phloem and other tissues, is gradually thrust outwards as the cambium adds to the secondary xylem. The cambium-cells on the inner side of each primary phloem bundle are active whilst the rest are still forming and, owing to this, the cambium-layer as a whole, which was at first a wavy band (in transverse section), soon becomes circular.

The cambium cells lying just outside the primary xylem, instead of giving rise to secondary xylem and phloem, usually produce strands of parenchyma—the *main* (also called primary) *medullary rays*—radiating outwards through the secondary xylem and phloem from the tips of the protoxylem groups. If a very compact secondary xylem is formed, it may be difficult to detect the primary xylem groups, or the main medullary rays. Small secondary medullary rays also are formed from the cambium cells. Annual rings of secondary wood can be recognised, but are not so distinct and well-defined as in the stem.

If the primary structure and the subsequent development be borne in mind, it is evident that the primary phloem bundles should be found just outside the secondary phloem on radii alternating with the primary xylem groups; but, frequently, as in the stem, they are more or less disorganised and indistinct.

If there is any considerable secondary growth, the pericycle, sooner or later, becomes completely meristematic, and forms a **phellogen.** This phellogen produces cork externally, and usually also, internally, a considerable amount of phelloderm (as in most deep-seated phellogens). Lenticels may be developed. The endodermis and cortical tissue die. It is comparatively rarely in roots that the phellogen has a superficial origin.

10. Anomalous Secondary Growth

In the roots of a few Dicotyledons the first cambium ring after a time becomes inactive, and a new cambium arises in the pericycle or in the phelloderm. This in its turn, after producing a ring of xylem and phloem, is similarly replaced. In this way a series of concentric rings, consisting of secondary xylem and phloem, is formed in the root. This can be observed in the root of the beet.

11. Development of Lateral Roots (Fig. 95)

Normal root-branches are usually developed, in Angiosperms, entirely from the pericycle. The cortical tissue of the parent-root takes no part in the formation of the tissues of the lateral branch. This development from a deep-seated layer is called **endogenous.**

The development begins some little distance behind the apex of the parent-root, but before secondary growth has set in. The young lateral roots generally make their appearance in the pericycle just outside the protoxylem groups, so that the number of longitudinal rows of lateral roots usually corresponds to the number of xylem rays in the stele. Thus, if there are four xylem rays, there will usually be four longitudinal rows of normal lateral branches.

When development begins, two or more cells of the pericycle divide, *i.e.* become meristematic, and produce a growing-point, which soon shows a distinction into root-cap, dermatogen, periblem, and plerome. The young branch-root gradually elongates, stretching and then breaking the endodermis and overlying cortical tissue till it reaches the surface of the parent-root. The structure of the lateral root is identical with that of the parent-root, and the conducting tissues of the former make contact with those of the latter.

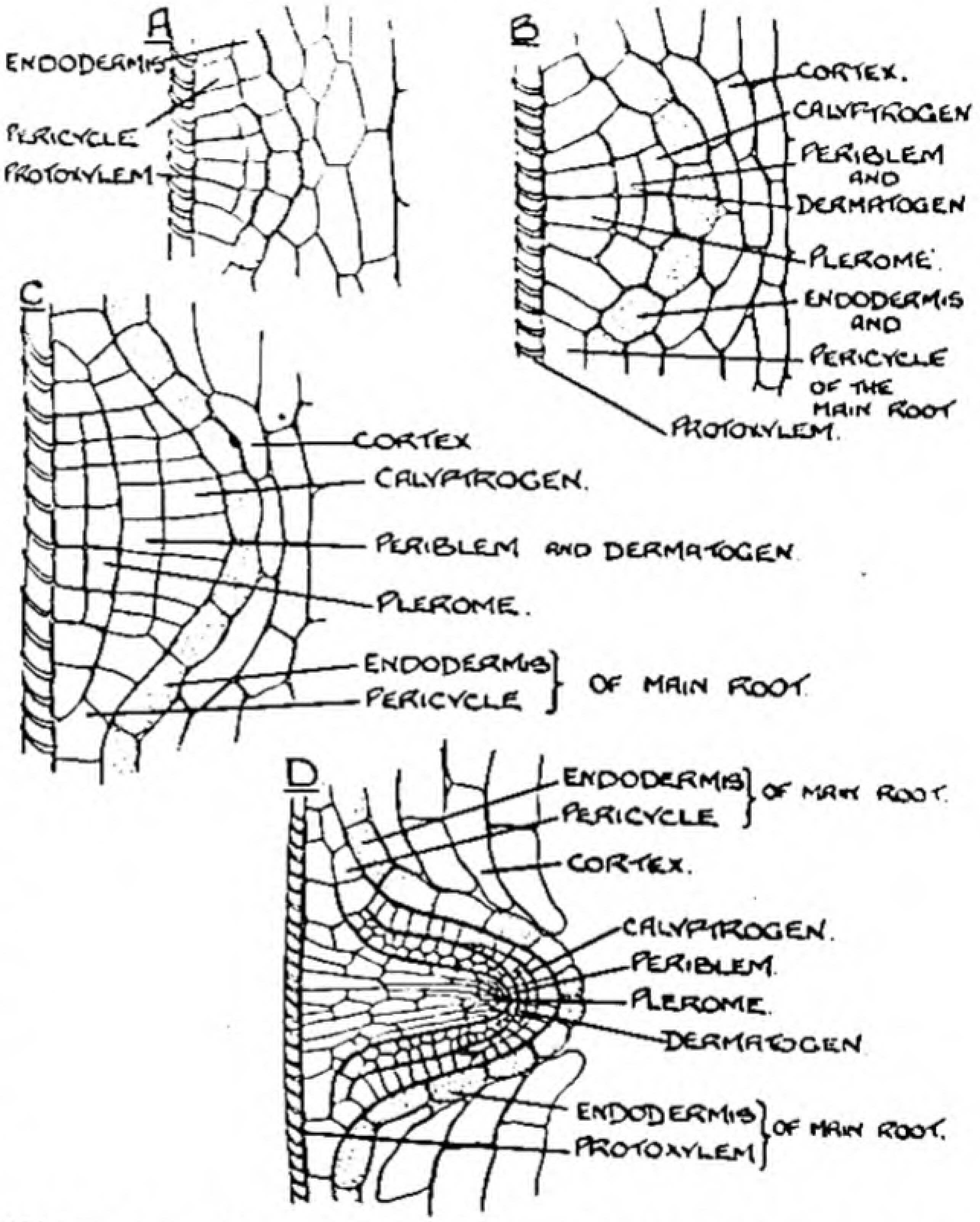

A
ENDODERMIS
PERICYCLE
PROTOXYLEM
B
CORTEX.
CALYPTROGEN
PERIBLEM AND DERMATOGEN
PLEROME.
ENDODERMIS AND PERICYCLE OF THE MAIN ROOT
PROTOXYLEM.
C
CORTEX
CALYPTROGEN.
PERIBLEM AND DERMATOGEN.
PLEROME.
ENDODERMIS
PERICYCLE
OF MAIN ROOT
D
ENDODERMIS
PERICYCLE
OF MAIN ROOT.
CORTEX.
CALYPTROGEN.
PERIBLEM.
PLEROME.
DERMATOGEN
ENDODERMIS
PROTOXYLEM
OF MAIN ROOT.

Fig. 95. STAGES IN THE DEVELOPMENT OF A LATERAL ROOT (Diagrammatic).

In Dicotyledons it is evident, considering the points at which the rootlets are developed, that after secondary growth has begun they will be seen (in a transverse section) radiating out from the tips of the primary xylem rays, and therefore running through the main medullary rays. When secondary growth takes place the cambium of the lateral root connects with that of the main root and further development is similar to that obtaining in stems and their branches.

Adventitious Roots are developed similarly. If they are developed from the stem, they originate in the pericycle. The horticultural practice of " striking " cuttings depends for its success on inducing adventitious roots to form near the base of shoots that are inserted in soil, sand or other moist, well aerated medium.

12. Exceptional Cases

Not uncommonly lateral rootlets are developed from the pericycle opposite the phloem bundles, e.g. in many grasses where the pericycle is wanting opposite the protoxylem, and in many Umbelliferae where an oil-duct lies in the pericycle opposite each protoxylem group. Often when the stele is diarch there are four rows of lateral rootlets, two being developed opposite the phloem.

13. Secondary Growth in Monocotyledons

True secondary growth is found in the roots of *Dioscorea* and *Dracaena*. The cambium ring originates in the cortex, and develops as in the stem. There is also cork-formation, the phellogen originating in the superficial cortical tissue beneath the piliferous layer. There are a few other monocotyledonous plants in which a periderm occurs in the roots (Liliaceae, Araceae).

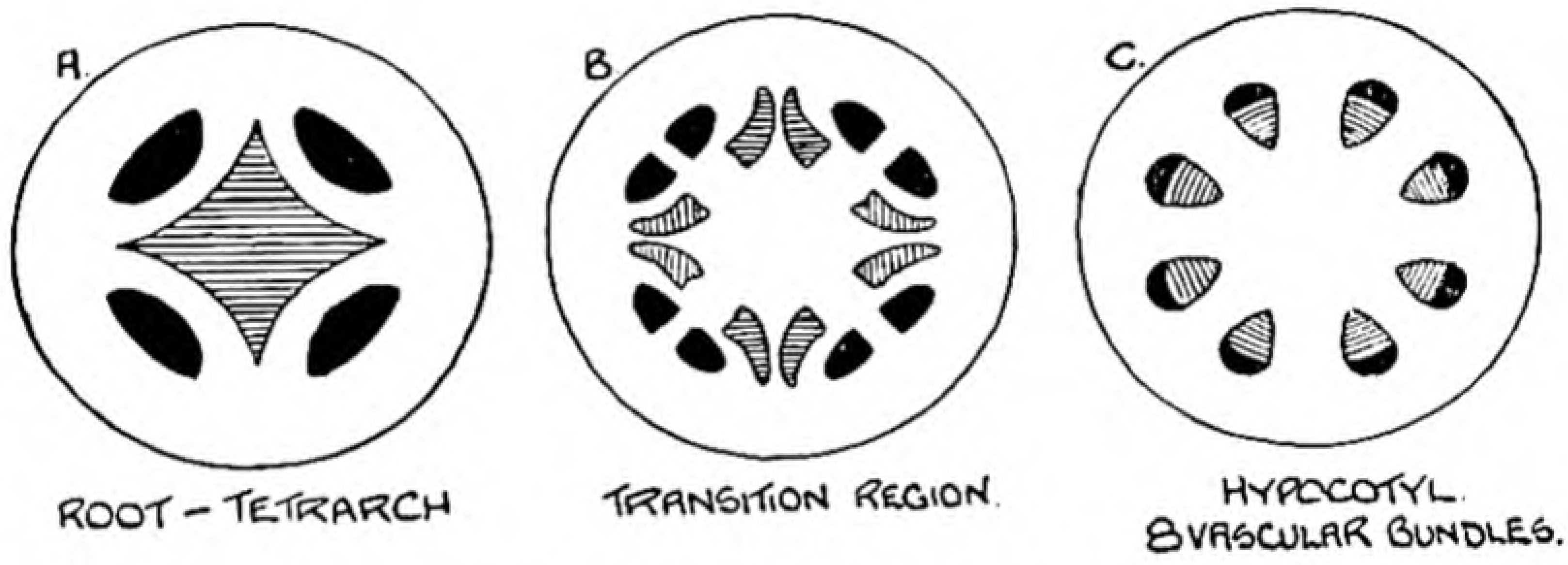


Fig. 96. Transition from Root to Hypocotyl in Seedling of *Ricinus*.

In roots which have no secondary thickening the hypodermis may develop into a protective exodermis by the cutinisation or suberisation of its cell-walls. The underlying cells of the cortex may reinforce this function by similar changes in their cell-walls. This is seen in many monocotyledonous and some dicotyledonous roots.

14. Functions of the Pericycle

The pericycle is an important layer in the root, and the functions discharged by it should be carefully noted. Its cells have a great capacity for remaining or becoming meristematic. In both Monocotyledons and Dicotyledons, as we have seen, lateral roots originate in this layer, and, in most Dicotyledons, it helps in the formation of the cambium-layer, and later may give origin to the phellogen.

15. Transition from Root to Stem—the Hypocotyl (Fig. 96)

We have already stated that the vascular system is continuous in root and stem. It is evident that the transition from the arrangement characteristic of the root to that characteristic of the stem is effected in that region of the axis which lies between typical stem and typical root. This region is the *hypocotyl.*

The length of the transition region, its position in the hypocotyl and the behaviour of the vascular strands vary considerably in different plants. In any seedling the position of the transition region may be found by cutting transverse sections of the hypocotyl at short intervals between the insertion of the cotyledons and the base of the primary root. Having thus found the site of the transition region, the changes which take place in it can be studied by cutting serial transverse sections and placing them in order upon glass slides for microscope study.

The conditions seen in the seedlings of runner bean and castor-oil plant is illustrated (Fig. 96). The primary root is tetrarch. Each group of xylem and of phloem splits radially into two. One half-phloem group and one half-xylem group become the xylem and phloem of a collateral, endarch stem bundle. In order to achieve this, each half-xylem group in the root gradually turns through 180° and brings the protoxylem from the exarch to the endarch position.

CHAPTER VI

THE LEAF OF THE ANGIOSPERM

A. EXTERNAL CHARACTERS

1. Origin and Development of the Leaf

We have already noticed that the leaf arises as an exogenous outgrowth of the stem apex. It begins as a slight lateral protuberance and proceeds to grow and differentiate (Figs. 32, 47, 48). First the **leaf-base** becomes distinct from the rudimentary **lamina** (leaf-blade). In its further development the leaf-base may become thick and fleshy, forming a **pulvinus** (Fig. 97), or it may give rise to a **leaf sheath**, as in the grasses (Fig. 99, D), or produce **stipules** as in members of the Rosaceae, Leguminosae, etc. (Fig. 100, D, E). Whilst this is going on the **lamina** takes shape as a dorsiventral structure through which veins ramify. The lamina may be separated from the leaf-base by a **petiole** or leaf-stalk (Fig. 97). The mature leaf, therefore, is an organ morphologically dissimilar to the stem.

Normally the lamina is green and advantageously placed to receive the incident rays of light at right angles to its upper surface.

In this connexion the pulvinus and petiole play an important role, the former causing twisting, the latter elongating, so that the laminae of a given plant are exposed as fully as possible and form a pattern which is usually referred to as a **leaf-mosaic** (Fig. 97).

2. Various Types of Leaf Form

Leaves, however, perform innumerable functions and their form is equally varied. Several well-marked types are of general occurrence amongst the Angiosperms. They are as follows:—

(*a*) **Cotyledons.**—These have already been discussed (Chap. III). If they come above ground as the first assimilating leaves of the plant, they are much simpler in form than the foliage leaves developed later.

(*b*) **Scale-Leaves.**—Typically these are small, brown, membranous leaves devoid of chlorophyll. They are developed on many underground stems (e.g. rhizomes), and form the protective scales of many buds (Fig. 47). Their function is usually protective. They may serve to protect buds that are developed in their axils, or, in the case of bud-scales, they protect the inner rudimentary foliage leaves of the bud. In most cases they represent leaf-bases, petiole and lamina being absent, e.g. on many rhizomes, and in buds of horse-chestnut and sycamore; but bud-scales may be the stipules of foliage leaves (banyan), or the stipules of scale-leaves (*Fagus* and *Quercus*) or rudimentary laminae (*Syringa*). The nature of bud-scales can be determined by examining the opening buds in Spring. Sometimes scale-leaves function as reservoirs of storage material, as in many bulbs.

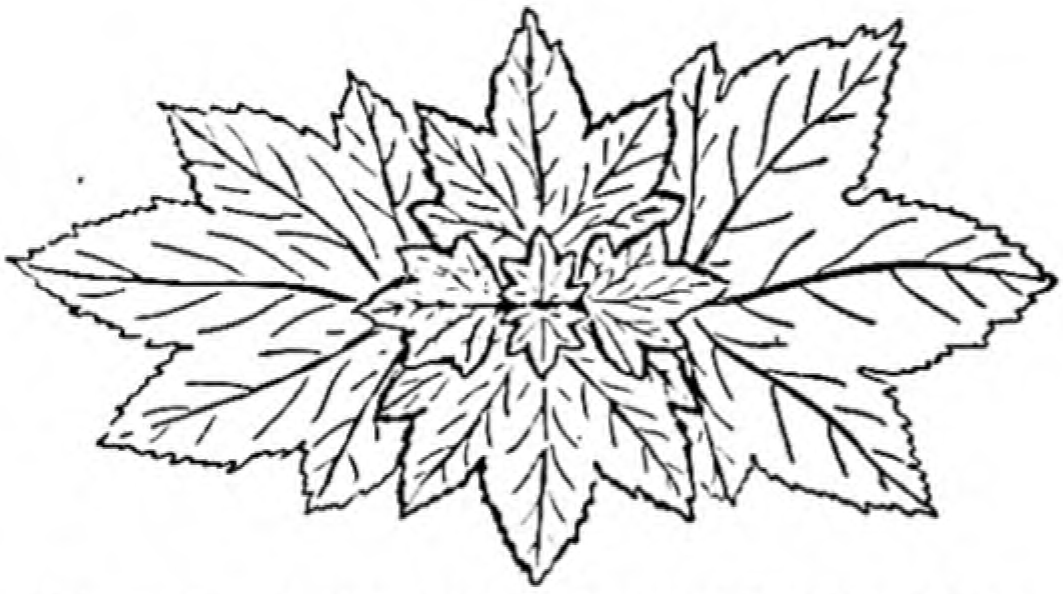


Fig. 97. LEAF-MOSAIC OF MAPLE (*Acer campestre*).

(*c*) **Foliage Leaves.**—These are the ordinary green leaves. They are the chief assimilating, and transpiring organs of the plant (Chap. I, §§ 7 and 8). Chlorophyll is present and is an essential factor in photosynthesis.

(*d*) **Bracts and Floral Leaves.**—These are specialised leaves borne on the reproductive shoots (floral region of the plant). They will be considered in connexion with the flower (Chap. IX).

In §§ 3–15 we illustrate a number of technical terms used in descriptive botany. They are intended for reference only. Many students may never need to use them. They belong to an era when botany consisted mainly of describing and classifying plants, and they are now used only in books in which external form must be clearly defined, as, for instance, in Floras and Pharmacopoeias. The student should pass on to § 14 at this stage.

3. General Descriptive Terms

If the petiole is present, the leaf is **petiolate** or stalked; if absent, **sessile.** If in a leaf the membrane runs vertically down the stem for some distance, the leaf is **decurrent** (Fig. 100, E). In grasses a ligule is developed on the base of the lamina, and the leaf is said to be **ligulate** (Fig. 99, D).

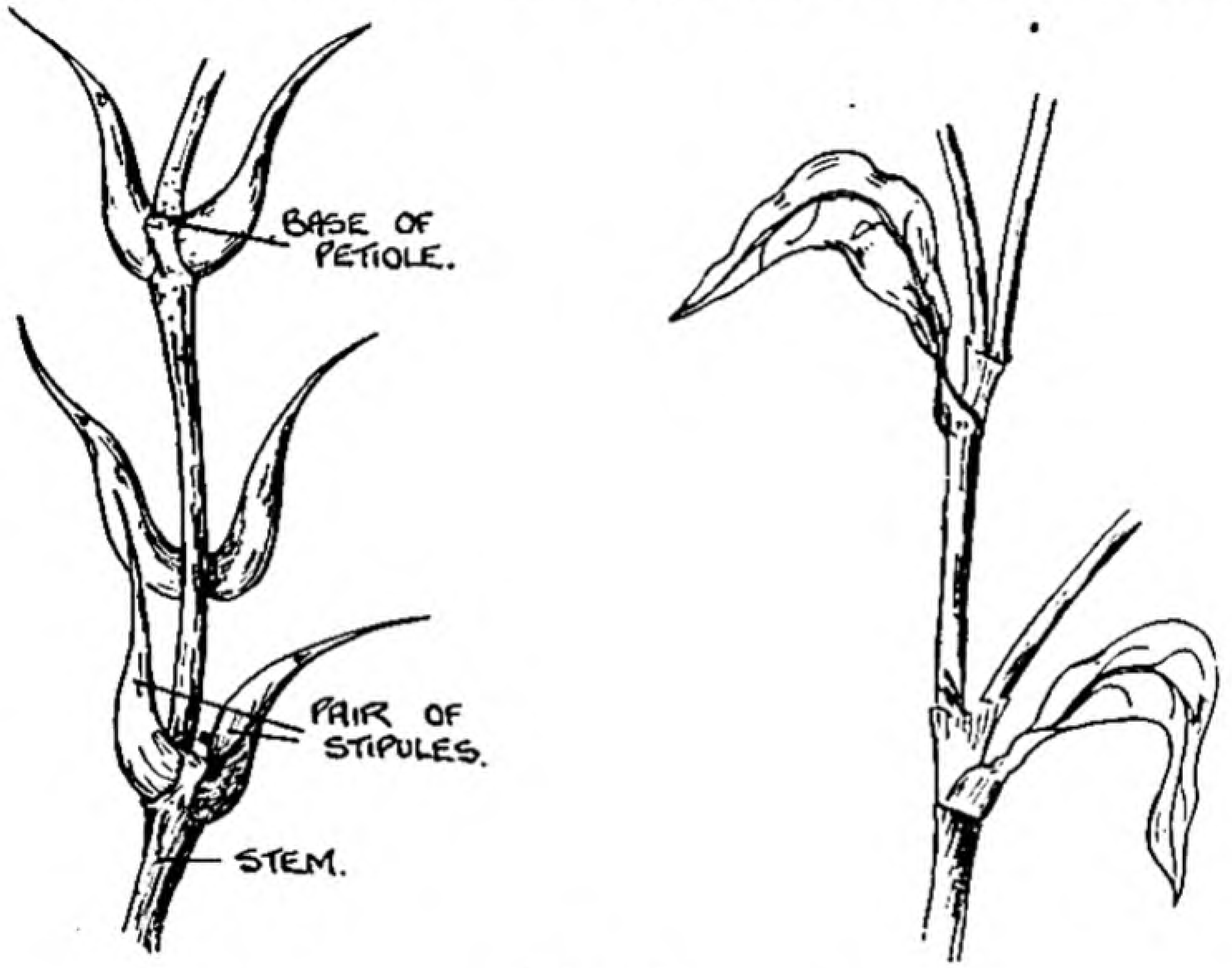


Fig. 98.

A, *Acacia*, stipular spines.

B, *Polygonum Bistorta*, ochreate stipules.

A leaf is **stipulate** or **exstipulate** according as stipules are present or absent. Stipules vary much in position, colour, size, and form. Sometimes they are large, green, and leafy (Fig. 100, F), showing the same development as an ordinary lamina (e.g. in the pansy); in this case they help in the work of photosynthesis. When the stipules are dry, small, pale, and membranous, they are usually functionless. In some buds (e.g. in the banyan), as already stated, they form the outer protective scales which fall off as the leaves expand. Occasionally the stipules are modified into spines, as in *Zizyphus Jujuba* (ber or bor) and *Acacia* (Fig. 98).

Various kinds of stipules are recognised. If they run up the base of the petiole for some distance, they are called *petiolar* (rose—Fig. 100, D). Where there is only one leaf at the node, if they run round to the other side of the stem and fuse there, an *opposite* stipule is formed (banyan); if their inner margins cohere between the leaf and the stem, an *axillary* stipule is formed; if they cohere in both ways, a tubular sheath called an **ochrea** (Fig. 98, B) is formed round the base of the internode (this is characteristic of plants belonging to the family Polygonaceae).

INSERTION OF THE LEAF.—The point at which a leaf-base joins the stem is called the *insertion* of the leaf. Leaves are described as *cauline* or *ramal* according as they are developed on the main stem or on the branches. Leaves developed on very short "reduced" stems (p. 76) so that they *appear* to come off from the root are called *radical* leaves (e.g. in *Taraxacum, Glossogyne, Senecio*).

4. Phyllotaxis

Two kinds of phyllotaxis (arrangement of leaves on a stem) are recognised: (*a*) **spiral,** (*b*) **cyclic** or **whorled.** In spiral phyllotaxis the leaves are developed one at each node, and are said to be **alternate** (Fig. 101, A). It is spoken of as the spiral arrangement, because, if a line were supposed to pass through the bases of the leaves in the order of their development, it would describe a spiral round the stem. In cyclic phyllotaxis two or more leaves form a *whorl* (Fig. 101, B) at each node; if two, the leaves are **opposite**; if more, **verticillate.** If in any one whorl the opposite leaves are placed immediately above those in the whorl below, so that there are only two vertical *rows* of leaves on the stem, they are said to be opposite and **superposed.** Usually, however, they are placed at right angles, so that there are four vertical rows of leaves; this is the opposite **decussate** arrangement (Fig. 97).

In spiral phyllotaxis the imaginary spiral line, following the order of development of the leaves, is called the **genetic spiral.** The angle of circumference between any one leaf and the next in order above it, in other words, the angle between the two *vertical* planes passing through these two leaves and the centre of the stem is the **angle of divergence.** Thus, suppose the alternate leaves are arranged in two opposite vertical rows (as in Fig. 97), evidently the divergence, or circumferential distance between any two leaves taken in order, is $\frac{1}{2}$, *i.e.* the angle of divergence is 180°. The vertical rows of leaves are called **orthostichies.**

Again, suppose, calling a particular leaf No. 1, five leaves are passed before coming to one, No. 6, lying immediately above No. 1, and that to reach No. 6 we have passed twice round the stem. Evidently the divergence is represented by $\frac{2}{5}$ (the whole circumferential distance divided by the number of leaves), and the angle of divergence is 144° (Fig. 101, C). The whole course gone through from leaf 1 to leaf 6 constitutes a *cycle.* There are five orthostichies. Thus to find the divergence divide the number of turns in a cycle by the number of leaves passed on the way, or by the number of orthostichies. For example, in a divergence of $\frac{1}{3}$, it is leaf No. 4 which lies above No. 1, and only one turn of the circumference is gone through; there are three orthostichies.

The divergences common in plants may be arranged in two series: (*a*) $\frac{1}{2}$, $\frac{1}{3}$, $\frac{2}{5}$, $\frac{3}{8}$, $\frac{5}{13}$ . . ., (*b*) $\frac{1}{4}$, $\frac{1}{5}$, $\frac{2}{9}$, $\frac{3}{14}$, $\frac{5}{23}$ . . . The student should notice the peculiar relation existing between the members in each series. Each fraction may be got by adding the numerators and denominators of the two preceding ones. Thus the series are easily remembered. The first series is the more important.

In cyclic phyllotaxis there is probably a number of genetic spirals running round the stem; thus, in the opposite decussate arrangement, two with a divergence of $\frac{1}{4}$.

5. Venation

The vascular bundles which pass into each leaf from the stem branch in the lamina and form the veins of the leaf. The veins not only convey water absorbed by the roots to the various parts of the leaf, and collect elaborated products, but they also have an important function in giving strength and support to the lamina, whose flattened form is advantageous for photosynthesis.

If the lamina is comparatively thin and membranous, we can recognise one or a number of chief veins as they give rise to projecting ridges or ribs on the under surface. But between these there are innumerable small veinlets running through the ground-tissue of the leaf and forming no projecting ridges. The character of the venation, *i.e.* the arrangement or appearance presented by the veins, depends chiefly on the number of prominent veins or ribs and the arrangement of the smaller veins or veinlets.

Two chief types are recognised in Angiosperms: (1) **reticulate venation,** characteristic of dicotyledonous leaves, though occurring also in a few Monocotyledons; (2) **parallel venation,** found in Monocotyledons only. In reticulate venation the veinlets between the larger veins run together irregularly to form a network (Fig. 116). In parallel venation the larger veins or the veinlets all run more or less parallel; no irregular network is formed (Fig. 102).

In both types the venation may be **unicostate** or **multicostate,** according as there is one chief vein (forming the midrib) or a number of chief veins. Figs. 47 and 97 show reticulate multicostate venation, Figs. 99, B, 100, B, 103, C, E, and G, unicostate.

6. Simple and Compound Leaves

The appearance presented by the lamina depends chiefly on the extent to which its membrane is developed *between the branches* of the vascular system. Sometimes it is completely developed, and the margin of the lamina is entire (Fig. 99, B). Usually, however, it is not completely developed. The extent to which it is incomplete varies considerably. Sometimes there are only small irregularities or cuttings of the margin, as in Figs. 103, C, E, and 104, A; frequently larger indentations called *incisions* are produced between the chief veins or branches.

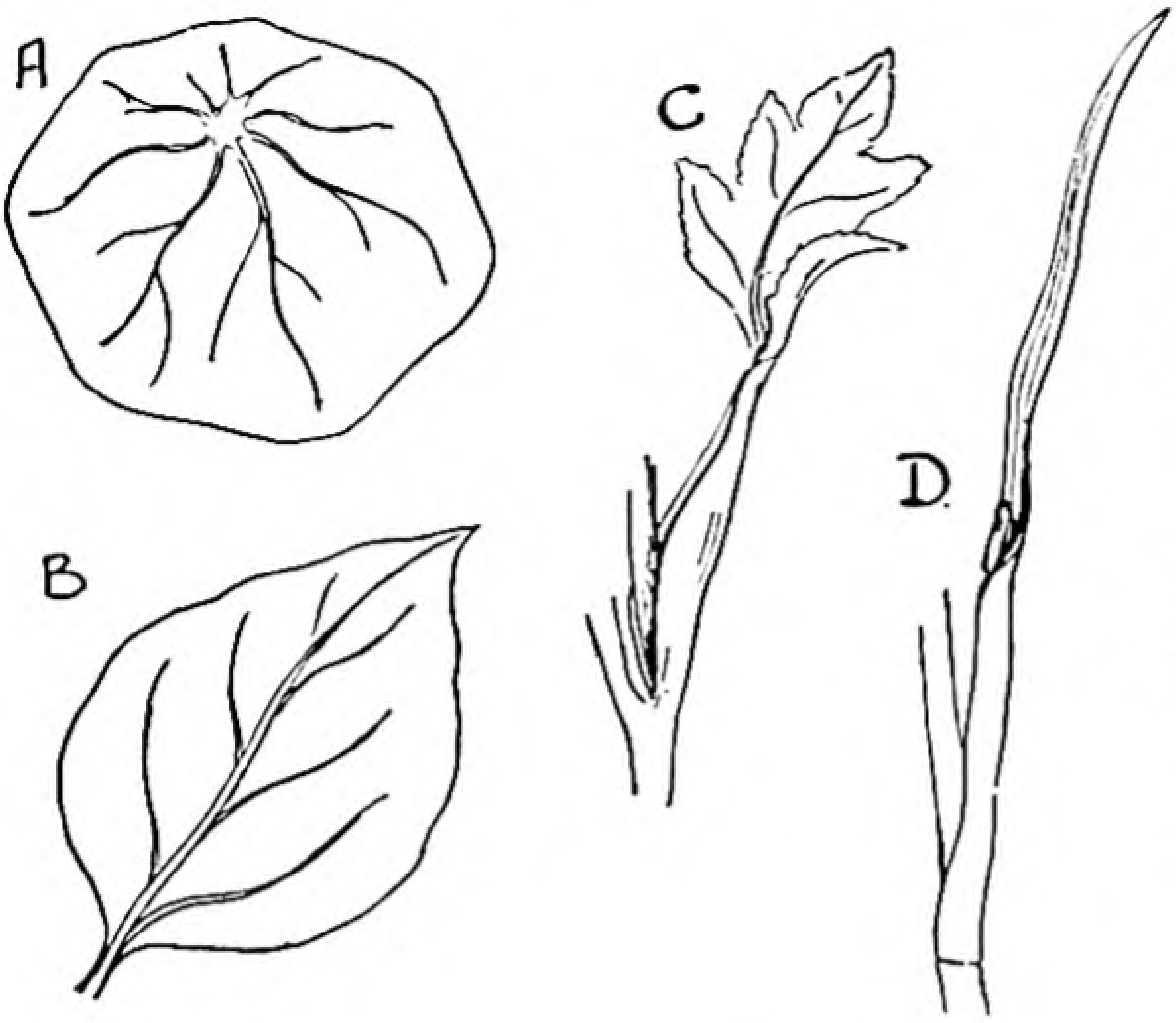


Fig. 99.

A, Peltate leaf of *Tropaeolum* (garden nasturtium);

B, Leaf of *Atropa Belladonna*, ovate, apex acuminate, lamina decurrent down petiole;

C, Amplexicaul leaf-base of *Angelica*;

D, Leaf of *Poa trivialis* (rough-stalked meadow-grass), linear, parallel venation, sheath with swollen base, ligule.

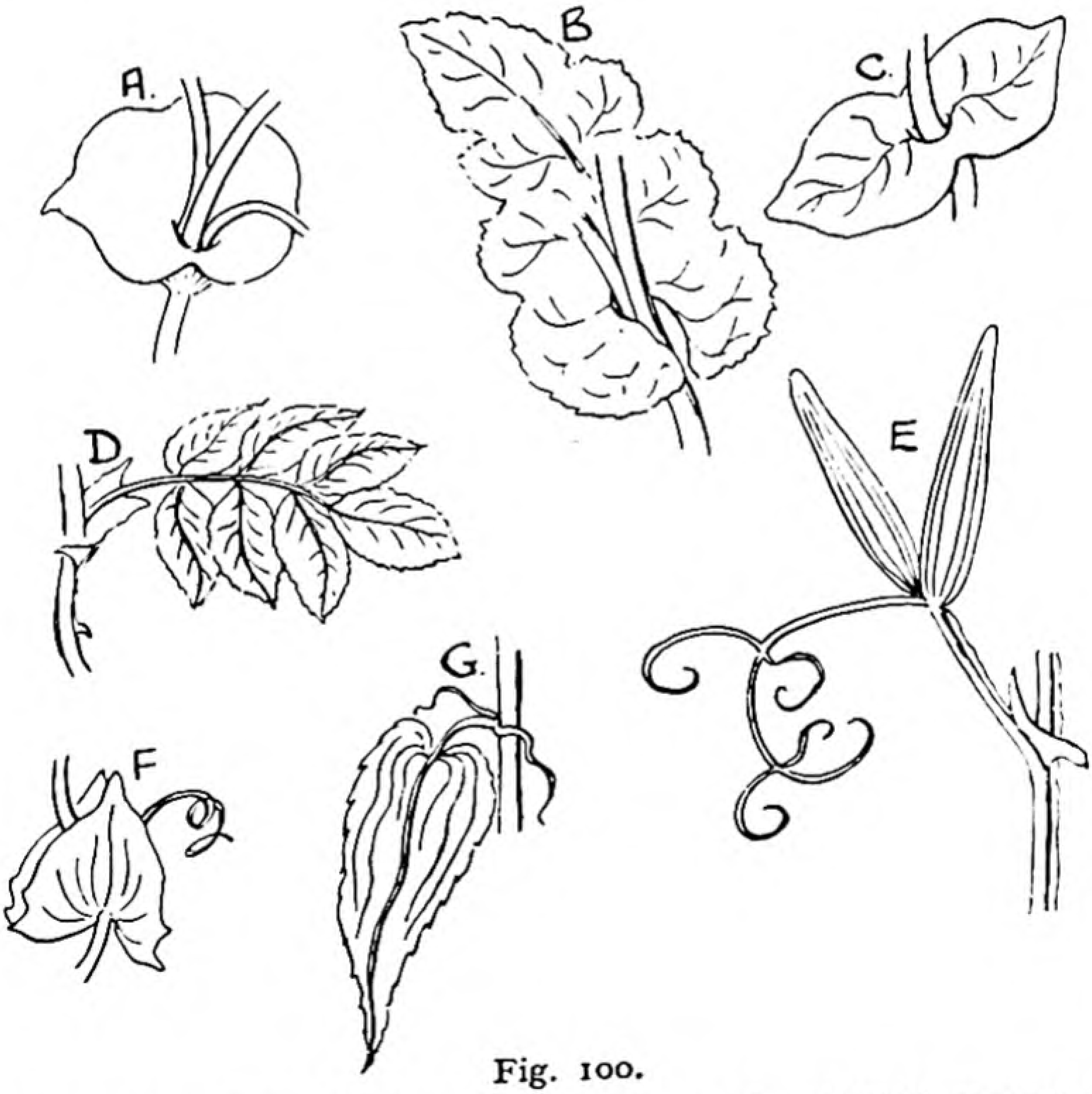


Fig. 100.

A, *Claytonia*, perfoliate leaf; B, *Sonchus oleraceus* (sow-thistle), upper leaf of shoot, base auriculate, margin dentate, teeth prickly; C, Connate leaves of *Lonicera caprifolium*; D, Leaf of *Rosa canina* (dog-rose), compound, imparipinnate, leaflets with serrate margins, stipules adnate to petiole, prickles; E, Leaf of *Lathyrus hirsutus*, compound, imparipinnate, leaflets (one pair only) linear-lanceolate, the rest modified as tendrils, petiole and stem winged, stipules; F, Leaf of *Lathyrus Aphaca* (yellow vetchling), leafy stipules, rest of leaf a tendril; G, *Smilax* leaf with pair of tendrils.

When the wing or membrane is not developed at all between the branches, the leaves are *compound*. All other leaves, in which the membrane is present to some extent, however little, between the branches, are *simple leaves*.

A compound leaf is one in which the lamina is broken up into a number of *separate* parts called leaflets, articulated at one point, or borne on a common stalk or rachis. A **simple leaf** is one in which the lamina is not split up into distinct leaflets. The leaflets of compound leaves in many respects resemble simple leaves.

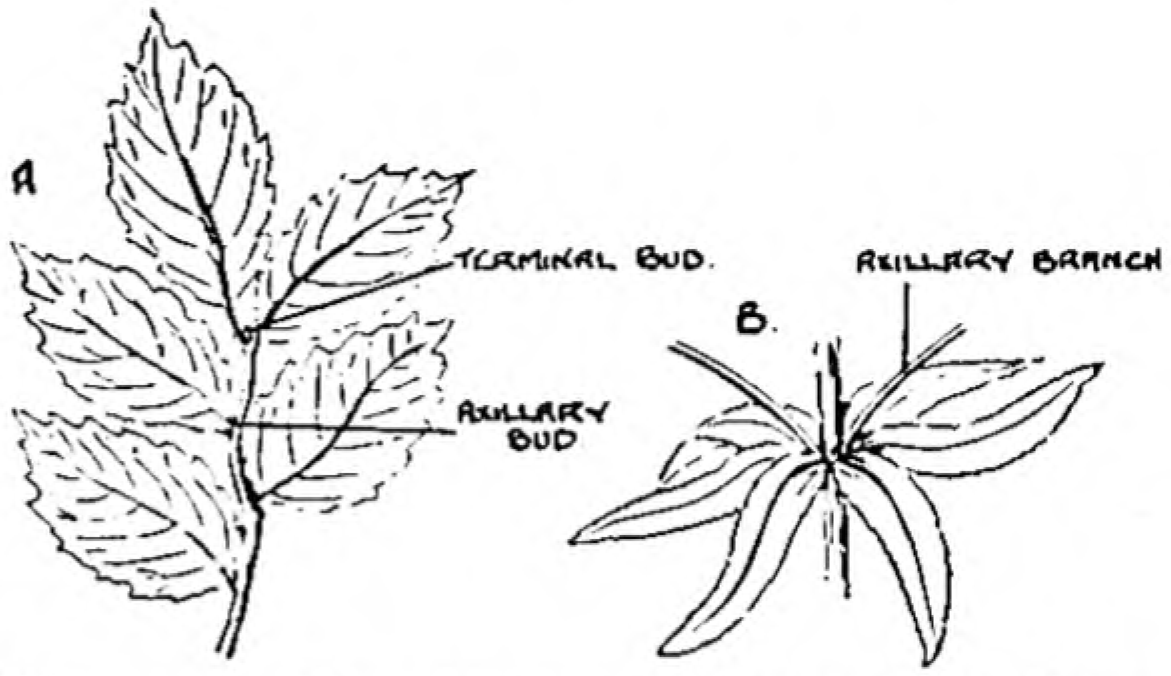


Fig. 101. ARRANGEMENT OF LEAVES ON STEM.

A. Alternate arrangement in *Ulmus* (elm); B. Whorled arrangement in *Galium aparine* (cleavers).

In the case of trees large leaves are frequently much divided or compound. The significance of this is partly that the leaves are thus protected from mechanical injury, more especially from the destructive action of the wind. This can be recognised by observing the leaves of many trees during a storm. But, apart from this, the sub-division of the lamina also prevents over-shading of the lower leaves borne on the plant.

The submerged leaves of aquatic plants are often much divided, e.g. water buttercup. The leaves are thus preserved from risk of mechanical injury, and, at the same time, present as large a surface as possible to the water. They are therefore able to carry on efficiently the process of photosynthesis.

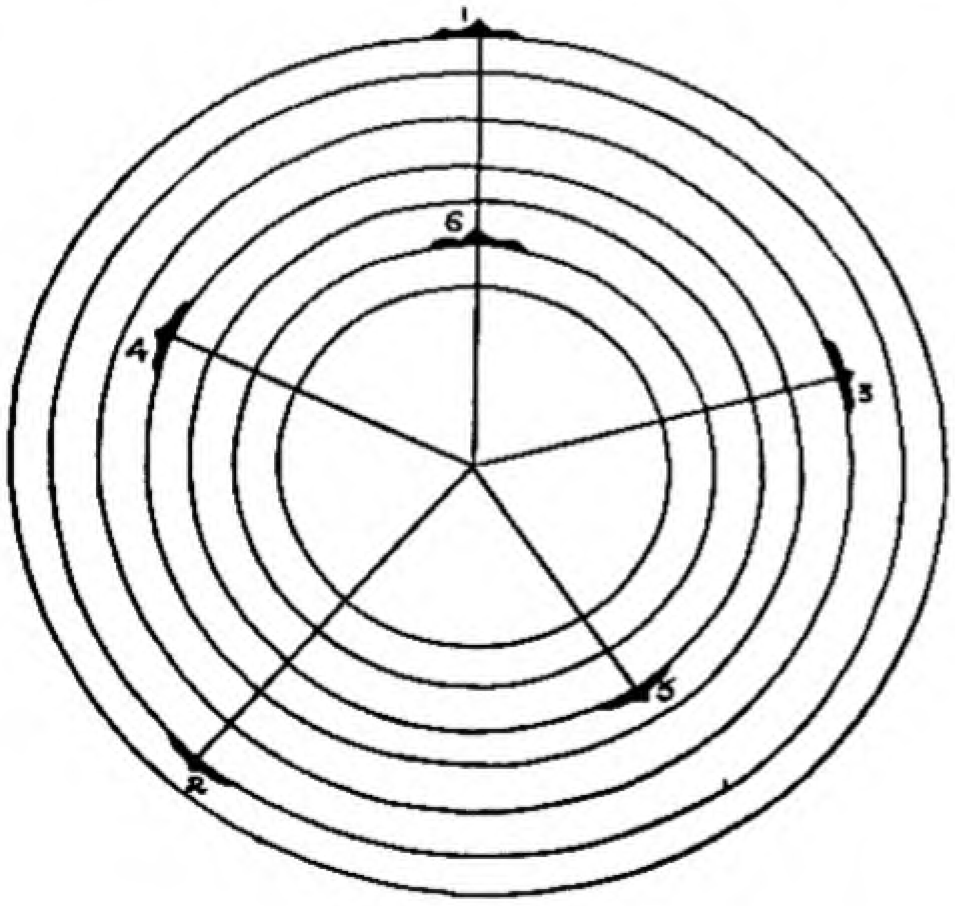


Fig. 101, c.

Plan of 2/5ths phyllotaxis.

7. Outline of the Lamina

Many terms are in use to describe the forms of outline presented by simple leaves or the leaflets of compound leaves. Those most frequently used are illustrated in the accompanying Figs. 103 and 104.

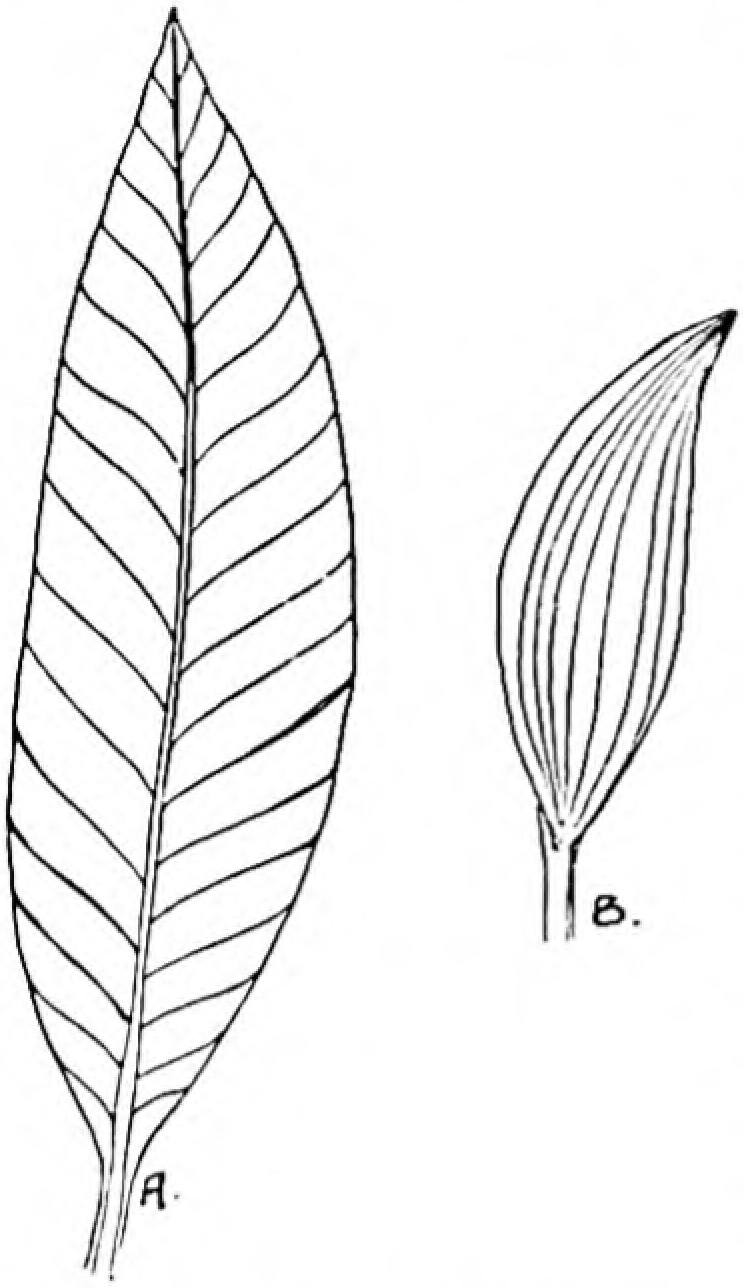


Fig. 102. PARALLEL VENATION.

A, Unicostate, *Musa* (banana);
B, Multicostate, *Allium ursinum*.

8. The Margin and Apex of a Leaf. Hairs

The **margin** of a leaf or leaflet is **entire** if it is perfectly even and shows no irregularities (Fig. 99, B); **serrate,** if it shows a number of sharp processes directed forward towards the apex (Fig. 103, C); **dentate,** or toothed, if these processes project outwards and are not directed forwards (Figs. 97, 100, B); **crenate,** if the processes are rounded (Fig. 104, A); **biserrate, bidentate, bicrenate,** if the processes themselves bear smaller secondary processes of the same kind; **spiny,** if the margin bears a number of hard, spiny processes resembling prickles (e.g. *Cnicus, Ilex*); **crisped,** or *curled,* if very wavy and irregular, as in the endive; **sinuate,** if the margin is more deeply indented (*Quercus,* Fig. 105, A). The sinuate margin forms a transition to the deeper cuttings of the margin, which are called incisions (§ 19).

The **apex** of a leaf or leaflet may be **rounded** (or obtuse—Fig. 103, D); if it comes to a point, it is **acute** (Fig. 103, C); if slender and very much drawn out, **acuminate** (Fig. 99, B).

Hairs.—The leaf may be hairy. If the margin of the leaf bears a fringe of fine hairs, it is described as **ciliate.**

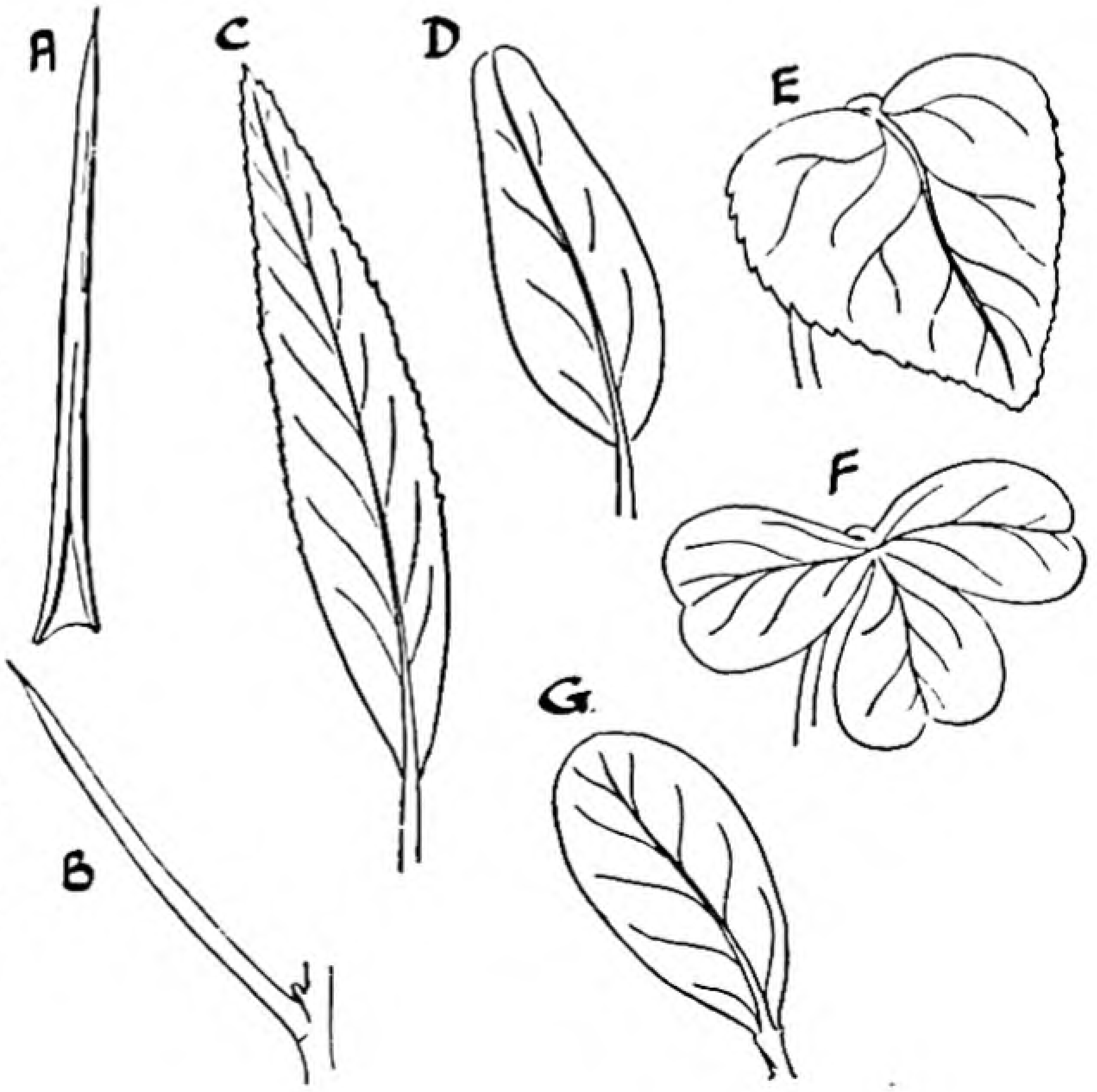


Fig. 103.

A, Subulate leaf of *Subularia aquatica* (water awl-wort);

B, Acicular leaf of *Hakea*;

C, Lanceolate leaf of *Salix fragilis* (crack willow), serrate margin, acute apex;

D, Oblong leaf of *Buxus sempervirens* (box), apex obtuse;

E, Cordate leaf of *Viola Riviniana* (dog-violet), margin crenate;

F, Obcordate leaflet of the ternate compound leaf of *Oxalis Acetosella*;

G, Obovate leaf of *Arctostaphylos Uva-ursi* (bearberry).

9. Incision of the Lamina

In a *unicostate* leaf, if the incisions do not pass half-way down to the midrib, the leaf is **pinnatifid** (Fig. 105, B); if rather more than half-way, **pinnatipartite** (Fig. 105, C); if *almost* to the midrib, **pinnatisect** (Fig. 105, D). Corresponding to these simple leaves, we have, where the incision is complete, the compound leaf of the **pinnate** type (Fig. 105, E). Similarly, where the venation is multicostate, we may have **palmatifid** (Fig. 97), **palmatipartite** (Fig. 106, A), or **palmatisect** (Fig. 106, B) simple leaves; and the corresponding compound leaf is of the **palmate** type (Fig. 47).

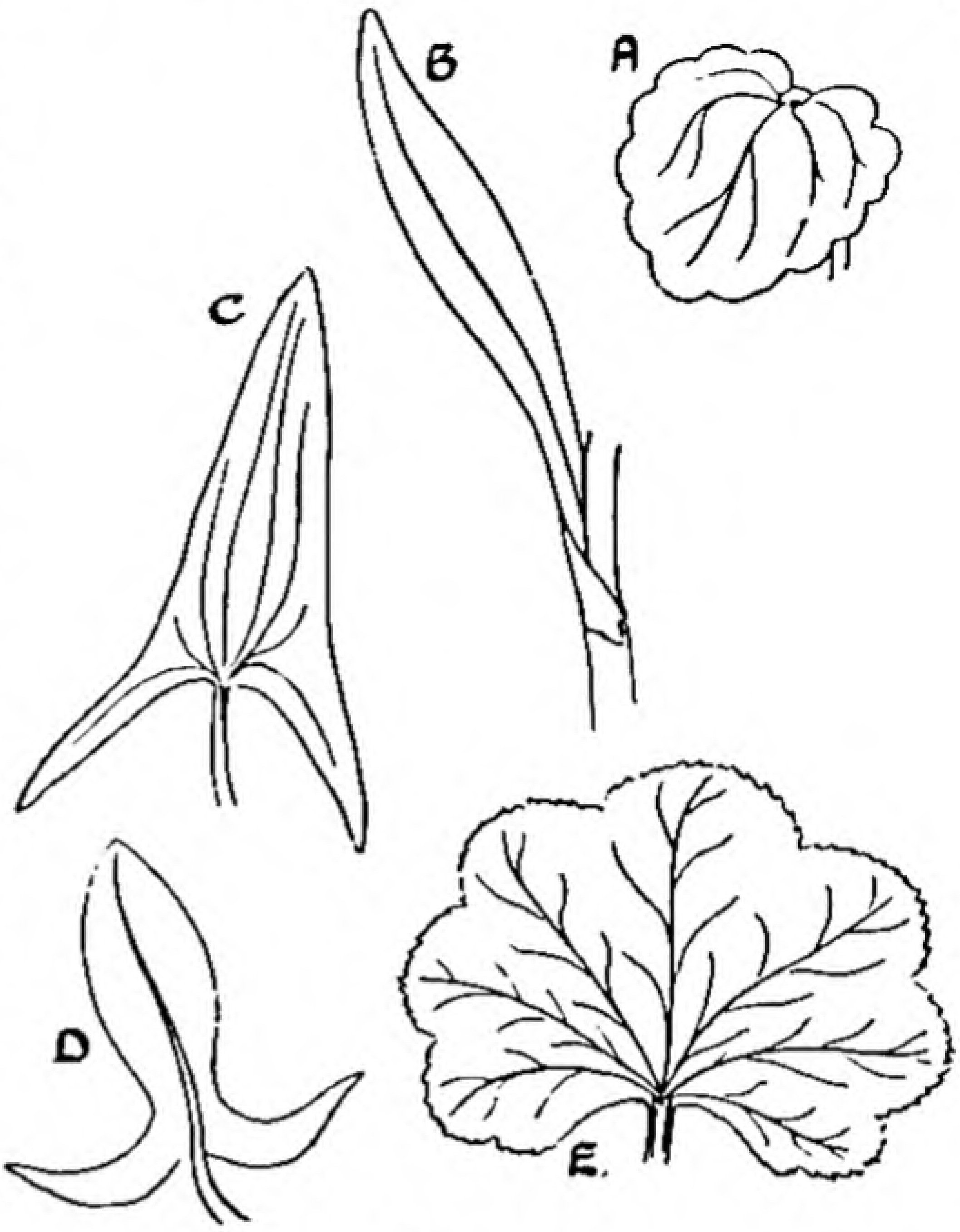


Fig. 104.

A, Reniform leaf of *Nepeta hederacea* (ground ivy), crenate margin; B, Spathulate leaf of *Aster Tripolium* (sea-aster); C, Sagittate leaf of *Sagittaria sagittifolia* (arrow-head); D, Hastate leaf of *Rumex Acetosella* (sheep's sorrel); E, Orbicular leaf of *Eranthis hyemalis* (winter aconite).

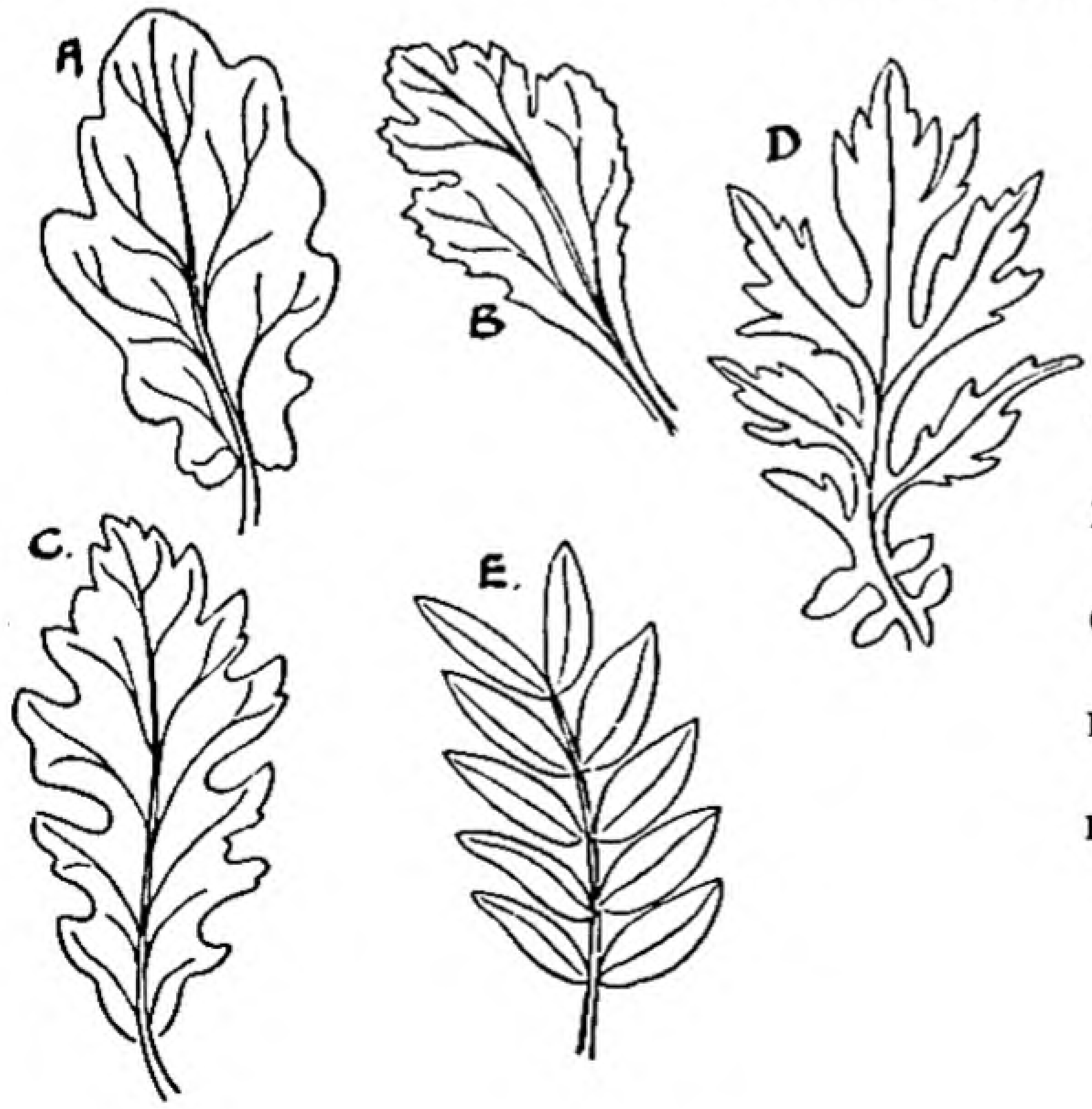


Fig. 105. Incision of Lamina: Pinnate Venation.

A, Pinnate leaf of *Quercus Robur*, sinuate margin;

B, Pinnatifid leaf of *Centaurea Scabiosa*;

C, Pinnatipartite leaf of *Quercus Cerris*;

D, Pinnatisect leaf of *Artemisia maritima*;

E, Compound paripinnate leaf of *Cassia angustifolia*, leaflets lanceolate.

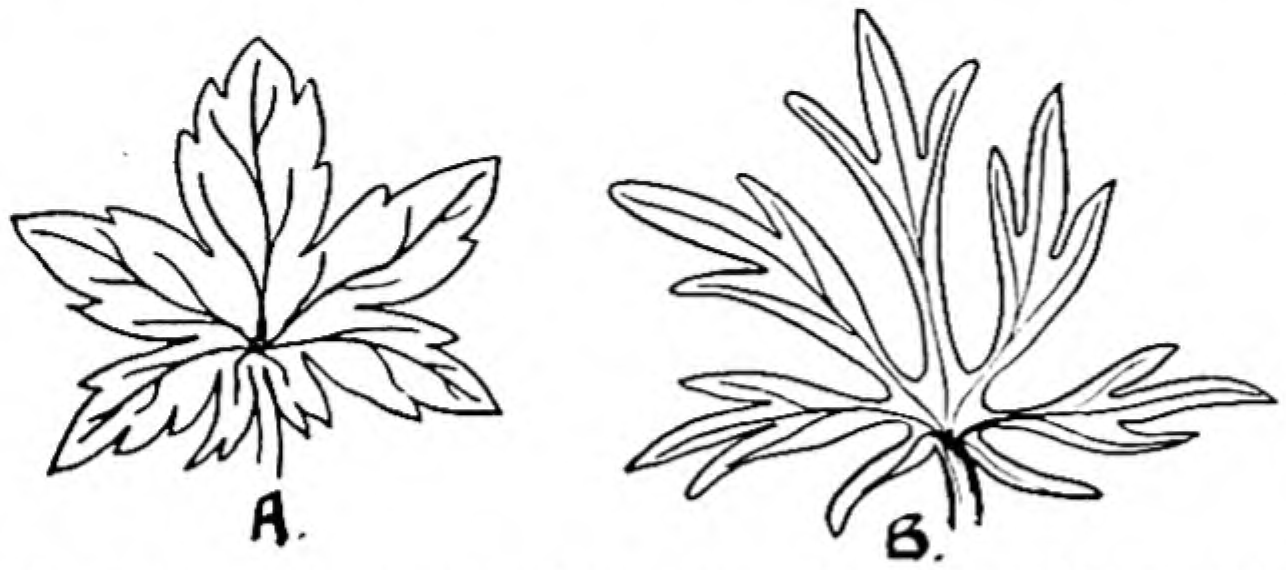


Fig. 106. Incision of Lamina: Palmate Venation.
A, Palmatipartite leaf of *Geranium pyrenaicum*;
B, Palmatisect leaf of *Geranium sanguineum*.

The terms pinnati-fid, -partite, -sect, palmati-fid, -partite, -sect are also applied to leaflets of compound leaves. If the divisions of a simple leaf are again incised, the terms **bi-pinnatifid,** etc. are used; or a pinnatipartite leaf may have divisions which are pinnatifid, etc.

When a unicostate leaf is incised in such a way that there is a large *rounded* terminal division with others which become gradually smaller towards the base, the leaf is said to be **lyrate** (Fig. 107, A). A **runcinate** leaf (e.g. *Taraxacum*, Fig. 107, B) is a pinnatifid leaf in which there is a large pointed terminal lobe, and the apices of the smaller lobes behind are directed backwards. In a multicostate leaf, where, as already indicated, the branching is of the cymose type, only daughter-branches of the first order, as a rule, are given off in a cymose fashion, as in Fig. 97; but occasionally these may again branch cymosely, as in Fig. 107, C. This is known as a **pedate** leaf.

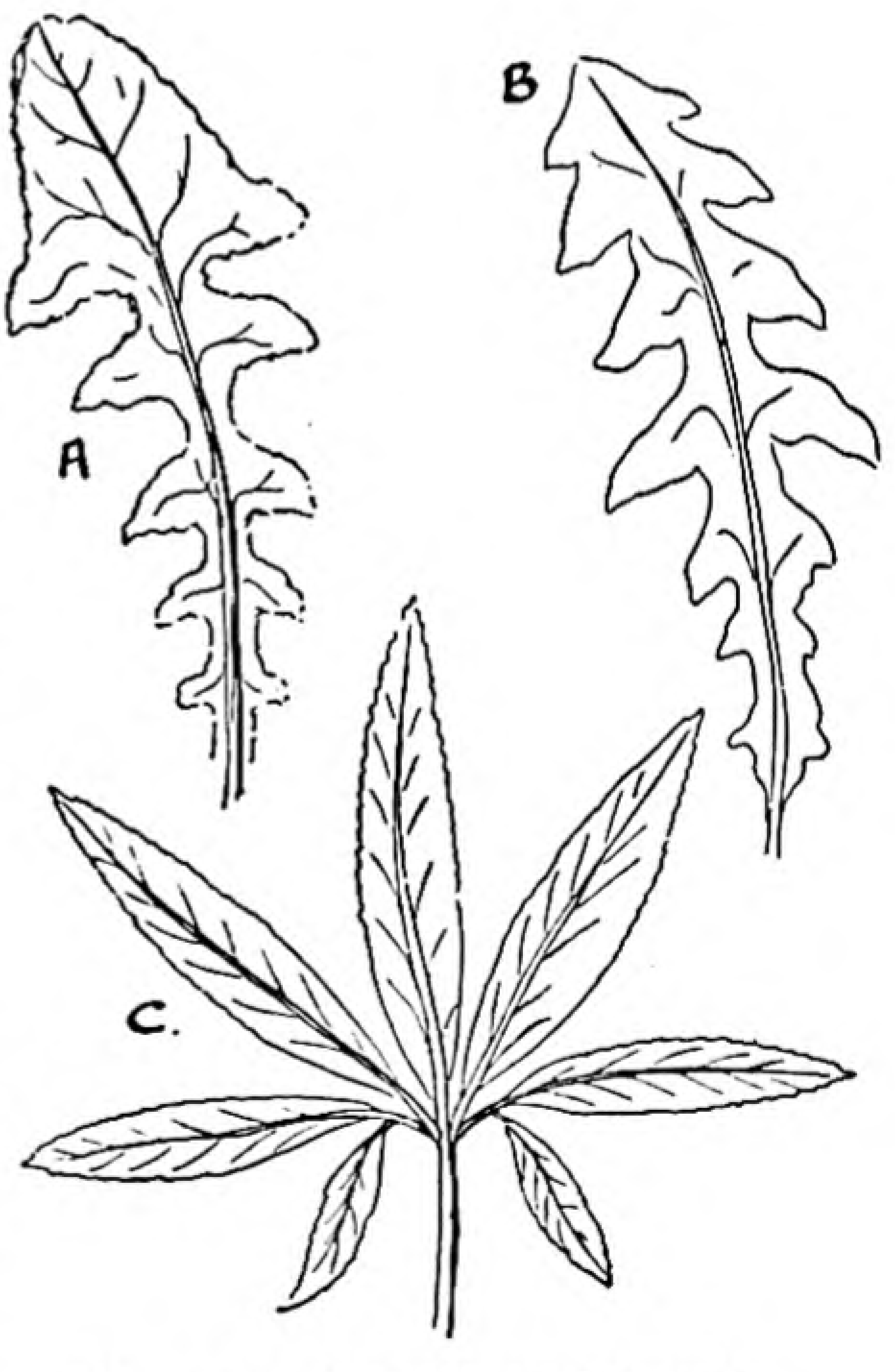


Fig. 107. Forms of Leaves.

A, Lyrate leaf of *Brassica arvensis* (charlock);
B, Runcinate leaf of *Taraxacum officinale* (dandelion);
C, Pedate leaf of *Helleborus fœtidus* (fœtid hellebore).

10. Compound Leaves

Often a compound leaf is mistaken for a stem bearing leaves. The following points of difference should be carefully noticed: (*a*) a compound leaf has no apical bud or growing-point; (*b*) it has a bud in its axil, and does not arise in the axil of a leaf; (*c*) it may have stipules, or an expanded sheath at the base; (*d*) the leaflets have no axillary buds.

There are certain special terms used in the description of compound leaves to which we must now refer. In the *pinnate leaf* the leaflets are borne on the common rachis or axis. Usually the leaflets are arranged in pairs, the leaflets of each pair being opposite each other. If an unpaired terminal leaflet is present, the leaf is described as **imparipinnate** (Fig. 100, D and E); if no terminal leaflet is present, so that the number of leaflets is even, the leaf is **paripinnate** (Fig. 105, E). The leaflets themselves may be completely incised. Here the secondary leaflets formed are called **pinnules**, and the leaf is said to be *bipinnate* (Fig. 108, A).

In a *palmate* compound leaf the leaflets come off at the same point. If there are two leaflets, the leaf is *bifoliate*, or *binate*; if three, *trifoliate*, or *ternate* (Fig. 103, F), and so on; if a large number, *multifoliate* (Fig. 47). Fig. 108, B shows a biternate leaf.

Citrus has a peculiar compound leaf, bearing only one leaflet. This is recognised as a compound leaf by the fact that the expanded lamina is distinctly articulated to the winged petiole (Fig. 109).

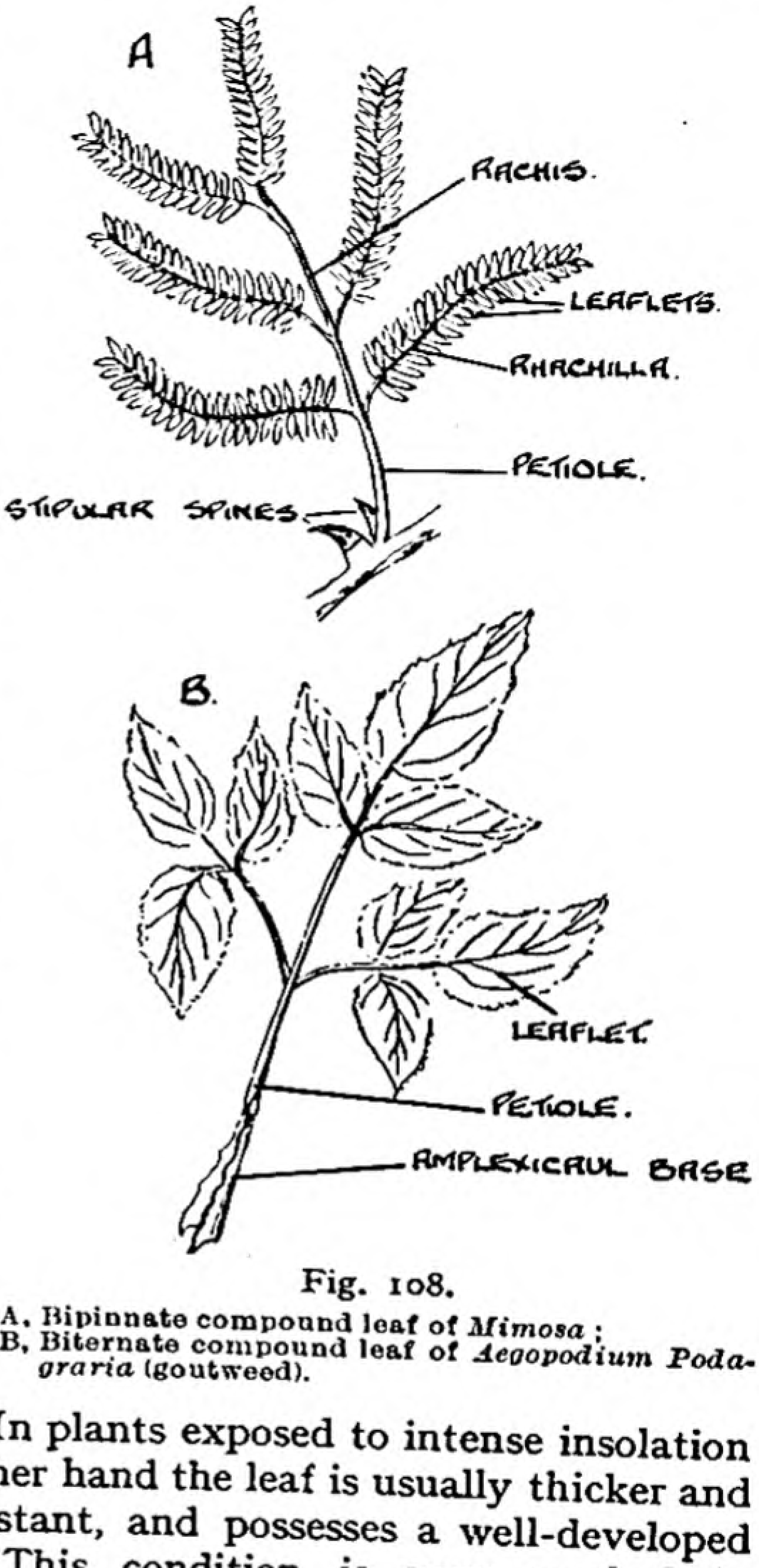


Fig. 108.

A, Bipinnate compound leaf of *Mimosa*;
B, Biternate compound leaf of *Aegopodium Podagraria* (goutweed).

11. Texture and Duration of Leaves

Shade- and moisture-loving plants usually have thin leaves with poorly developed cuticle. In plants exposed to intense insolation on the other hand the leaf is usually thicker and more resistant, and possesses a well-developed cuticle. This condition is very marked in the leaves of many tropical plants and in evergreen plants in temperate regions.

Leaves which are thin and membranous are described as *herbaceous*. Some are succulent and *fleshy*. The leaves are *caducous* if they fall off very early; *deciduous*, if they fall at the end of each season; *persistent*, if they remain on the plant for more than one season. Plants with persistent foliage leaves are *evergreens*.

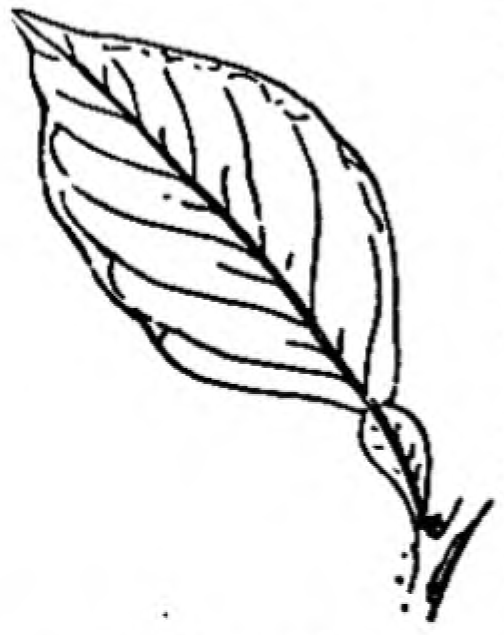


Fig. 109.

Unifoliate compound leaf of *Citrus Aurantium* (orange), winged petiole.

12. Prefoliation

The form and arrangement of the young leaves in the bud is termed prefoliation. Prefoliation includes (*a*) *Ptyxis*, or the form of the young leaves *in the bud*, *i.e.* the way in which they are folded or rolled on themselves; (*b*) *Vernation*, or the relation between the different leaves in the bud, *i.e.* the manner in which they are arranged with regard to each other. These points may be determined either by removing the leaves of a bud one by one, or, better, by taking cross-sections of the bud. In flower-buds **aestivation** is usually used in the same sense as vernation in vegetative buds.

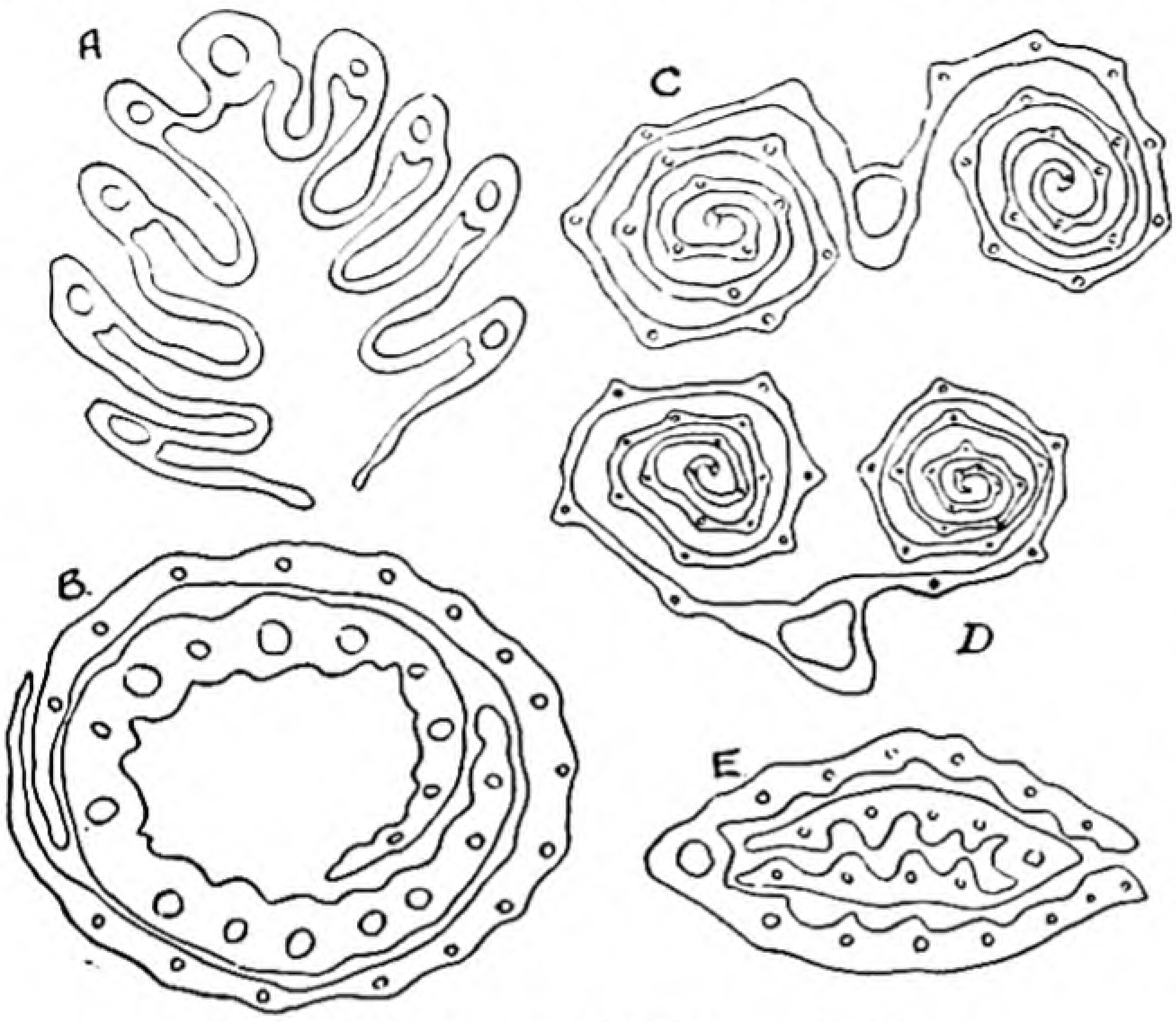


Fig. 110. PREFOLIATION: PTYXIS.

A, Plicate, beech; B, Convolute, foxtail-grass; C, Revolute, azalea; D, Involute, water lily; E, Conduplicate, equitant vernation, crested dog's-tail.

(All seen in transverse section of bud.)

(*a*) *Ptyxis of the Leaf* (Fig. 110).—It is *plane* if there is no folding or rolling at all; *conduplicate*, if folded lengthwise along the midrib, with the two halves face to face; *plaited*, or *plicate*, if there are numerous longitudinal folds; *crumpled*, if folded in all directions; *convolute*, if rolled from one margin to the other; *involute*, if rolled from both margins to the middle of the upper surface; *revolute*, if rolled similarly to the middle of the lower surface.

(*b*) *Vernation*.—Vernation (Fig. 111) is *valvate* if the young leaves touch each other laterally, but do not overlap; *imbricate*, if some overlap others, but not regularly; *twisted*, or *contorted*, if one margin of each leaf is directed inwards, and is overlapped, while the other margin is directed outwards, and overlaps the margin of the adjacent leaf.

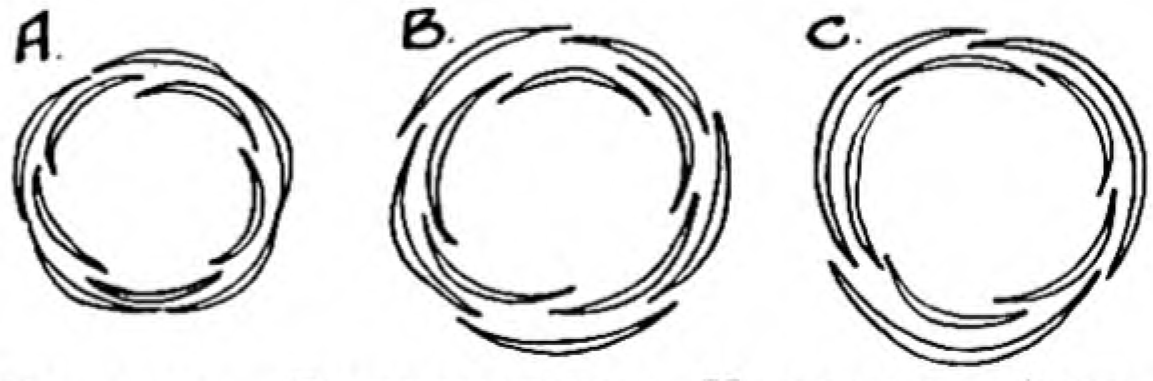


Fig. 111. PREFOLIATION: VERNATION (AND AESTIVATION).

A, Valvate calyx, imbricate corolla, *Prunus*;
B, Imbricate calyx and corolla, *Cassia*;
C, Twisted corolla, *Helianthemum*.

13. Special Modifications of Leaves

(*a*) Water storage leaves are found in many succulent plants. The leaf is usually very thick and only the peripheral regions are green and carry on the normal leaf functions. The bulk of the central region of the leaf consists of special water-storage tissue. As would be expected, we find leaves of this type on some plants inhabiting dry situations, and they are enabled to withstand extreme water shortage as they can draw on their internal water reserves during periods of drought. The aloes and agaves furnish examples of this type of leaf (see also Figs. 112, A, 139 and 140).

(*b*) **Leaf Tendrils.**—Leaves or parts of leaves frequently have the form of tendrils. The Leguminosae, Bignoniaceae and Cucurbitaceae furnish examples. In *Lathyrus hirsutus* (Fig. 100, E) the tendrils represent the upper leaflets of a compound imparipinnate leaf. Accompanying the reduction in leaf-surface that this entails we sometimes find, as in this vetch, " wings" developed on the stem so that the total surface available for photosynthesis is not reduced. In some species of Pea, e.g. *Lathyrus aphaca* (Fig. 100, F), the whole leaf is specialised to form a tendril, and the normal leaf functions are taken on by the greatly enlarged stipules. In *Gloriosa* (Liliaceae) the tip of the simple leaf is elongated to form a tendril. In *Smilax* (Liliaceae) the tendrils have been referred to as stipules, though it is more probable that they represent lateral organs due to the sub-division of the lamina into three parts of which only the middle one functions as a leaf.

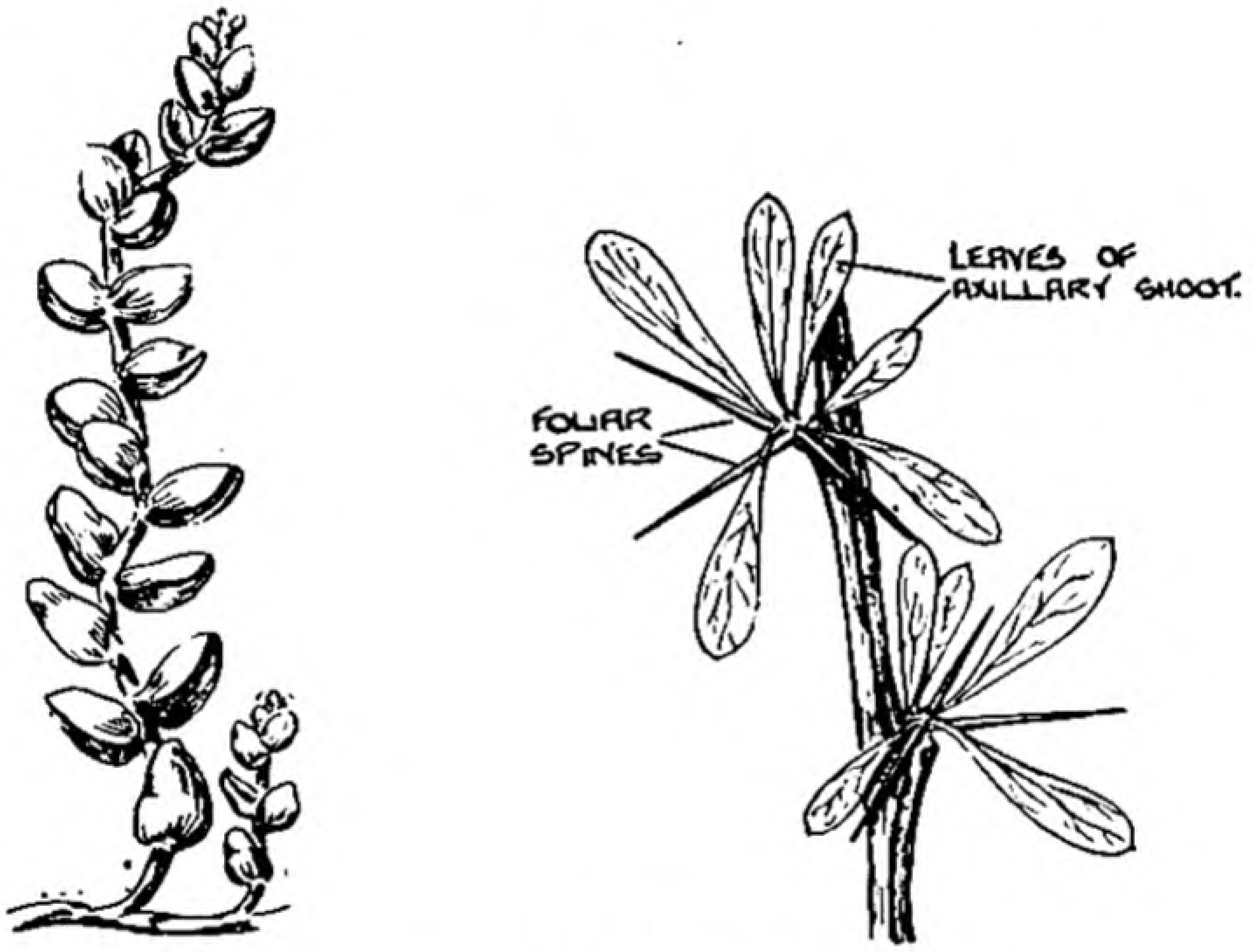


Fig. 112.

A, Shoot of *Sedum acre* (stonecrop), fleshy leaves.

B, Shoot of *Berberis* (barberry), leaf spines.

(*c*) **Leaf Spines.**—These may represent leaves or parts of leaves. The whole leaf may be modified into a spiny structure (Fig. 112, B), as in barberry (*Berberis*) where it is 3–5-rayed. In the seedling of gorse (*Ulex europaeus*, Fig. 112, C) the leaves are trifoliate, but in the adult plant the leaves are reduced to slender spines with a firmer branch-spine in each axil. In holly (*Ilex*) and the thistles the leaf margin forms a series of spines. In species of *Acacia* (Figs. 98, A, and 112, D), of *Zizyphus* and of *Euphorbia*, the stipules are represented by spines, whilst in *Azima* spines in the axils of normal leaves represent the leaves of lateral shoots (compare Cactaceae).

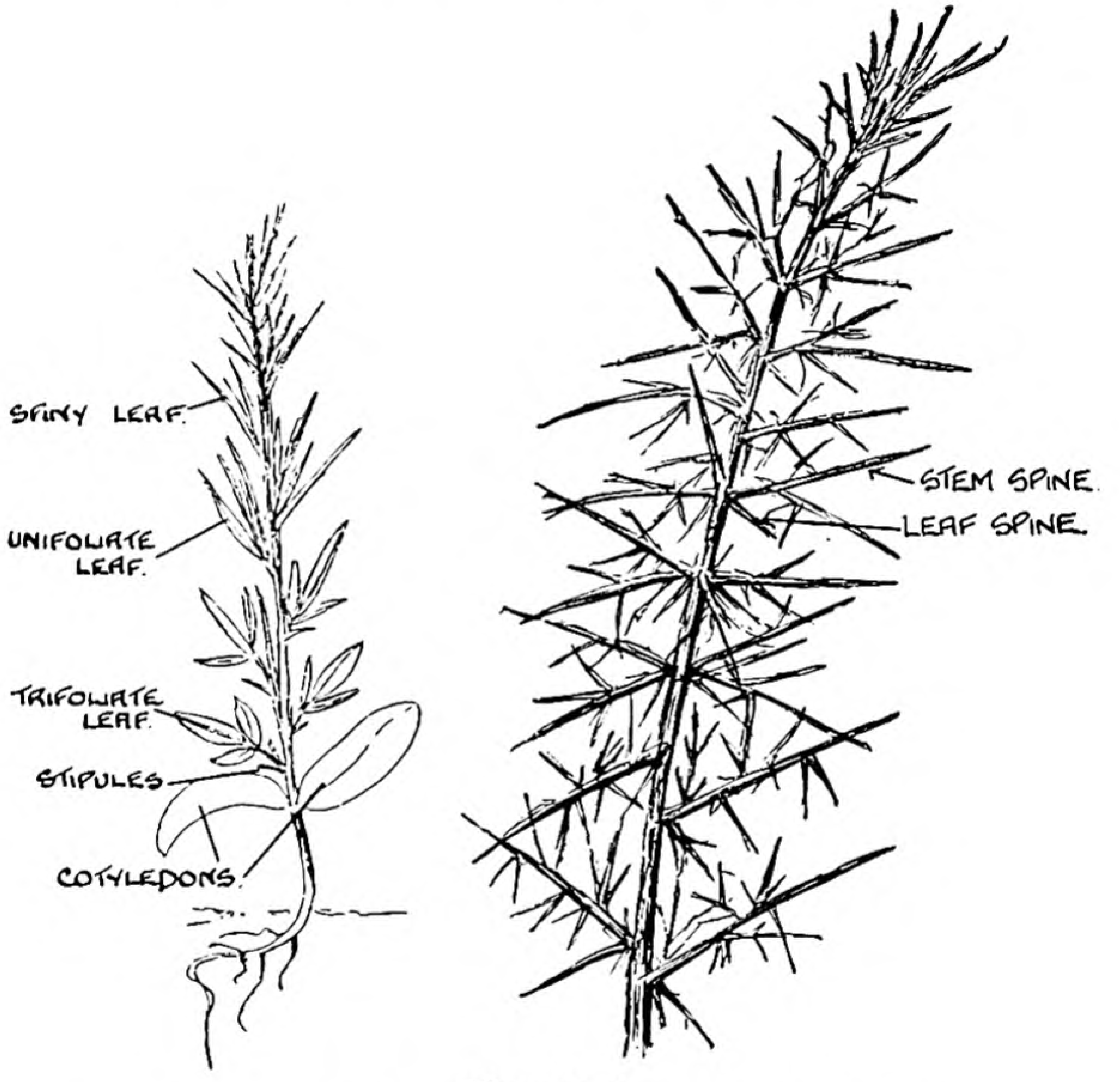


Fig. 112, C.

The seedling stage of *Ulex*.

The adult stage of *Ulex*.

(*d*) **Phyllodes.**—In some Australian species of *Acacia* the lamina of the leaf is absent, but the petiole is so flattened as to appear leaf-like. These flattened petioles are known as phyllodes and they are so developed as to place their surfaces in the vertical plane. Inspection shows the phyllode to be a leaf-structure, because there is a bud in its axil, but does not reveal that it is not a lamina turned edgewise. In young seedlings, however, normal compound leaves occur and the transition from normal leaf to phyllode can be traced, leaving no doubt as to the petiolar nature of the phyllode (Fig. 112, D).

(*e*) **Pitchers.**—In various insectivorous plants the leaves develop into pitcher-like structures, and show other peculiarities of form connected with their ability to trap and digest insects. We shall deal with these in more detail later (pp. 202, 203, Figs. 154 and 155).

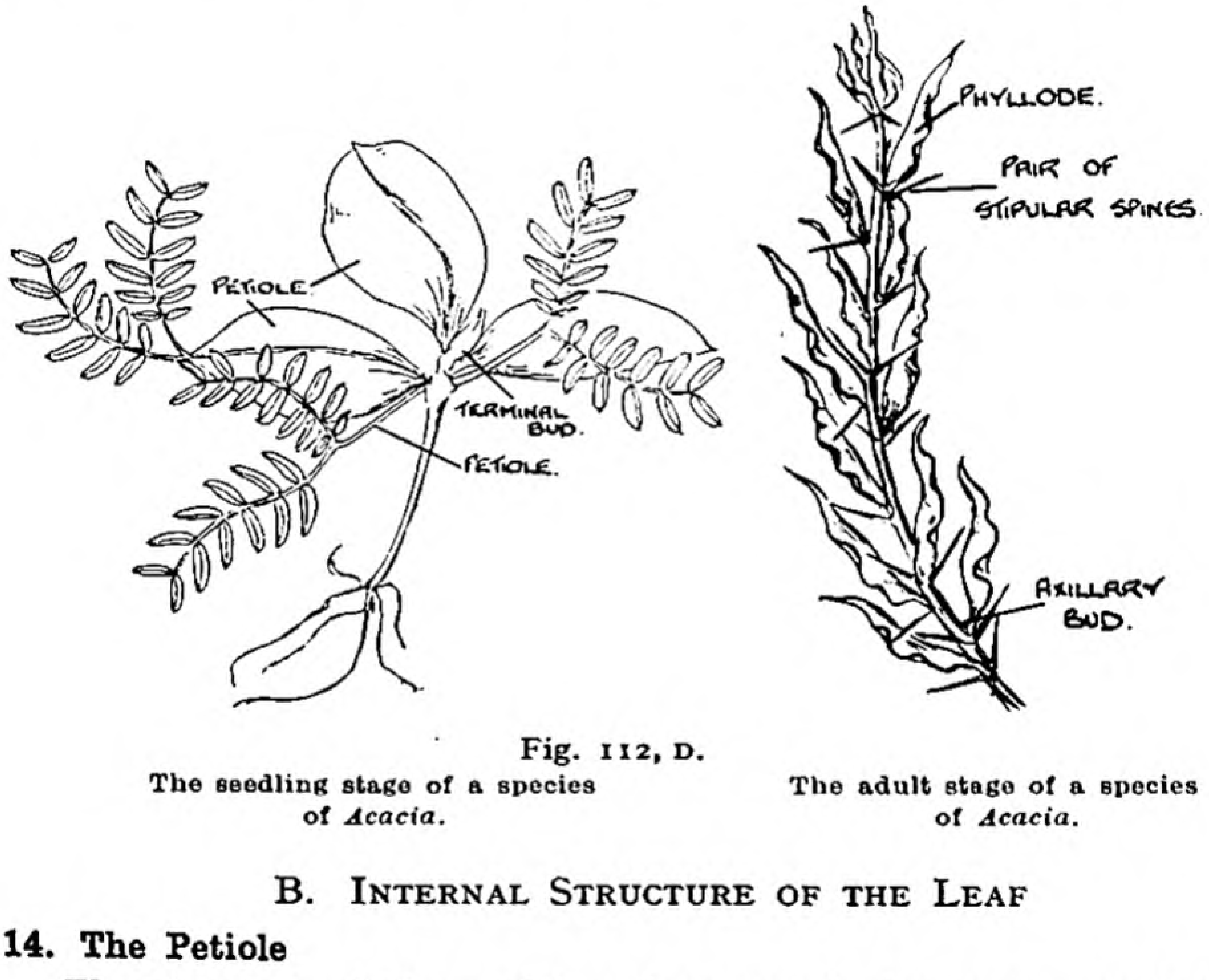


Fig. 112, D.

The seedling stage of a species of *Acacia*.

The adult stage of a species of *Acacia*.

B. Internal Structure of the Leaf

14. The Petiole

The structure of the petiole, when seen in transverse section, is frequently similar to that of the stem. It can only be distinguished in cases where the petiole shows a dorsiventral structure, e.g. when flattened, curved or grooved on its upper surface. In Angiosperms one (Fig. 113) or more (Fig. 67) collateral or bicollateral bundles pass from the stem into the leaf. As they do so they may divide into a number of smaller bundles whose arrangement may be crescentic or circular. Cambiform cells may separate xylem from phloem, but they are rarely actively meristematic.

The ground-tissue is essentially parenchymatous, but collenchyma and sclerenchyma are often present as in stems.

15. The Lamina—Bifacial (Dorsiventral) Type

We have chosen the leaf of privet (*Ligustrum vulgare*) as a suitable representative of a dorsiventral type of leaf. Fig. 113 shows

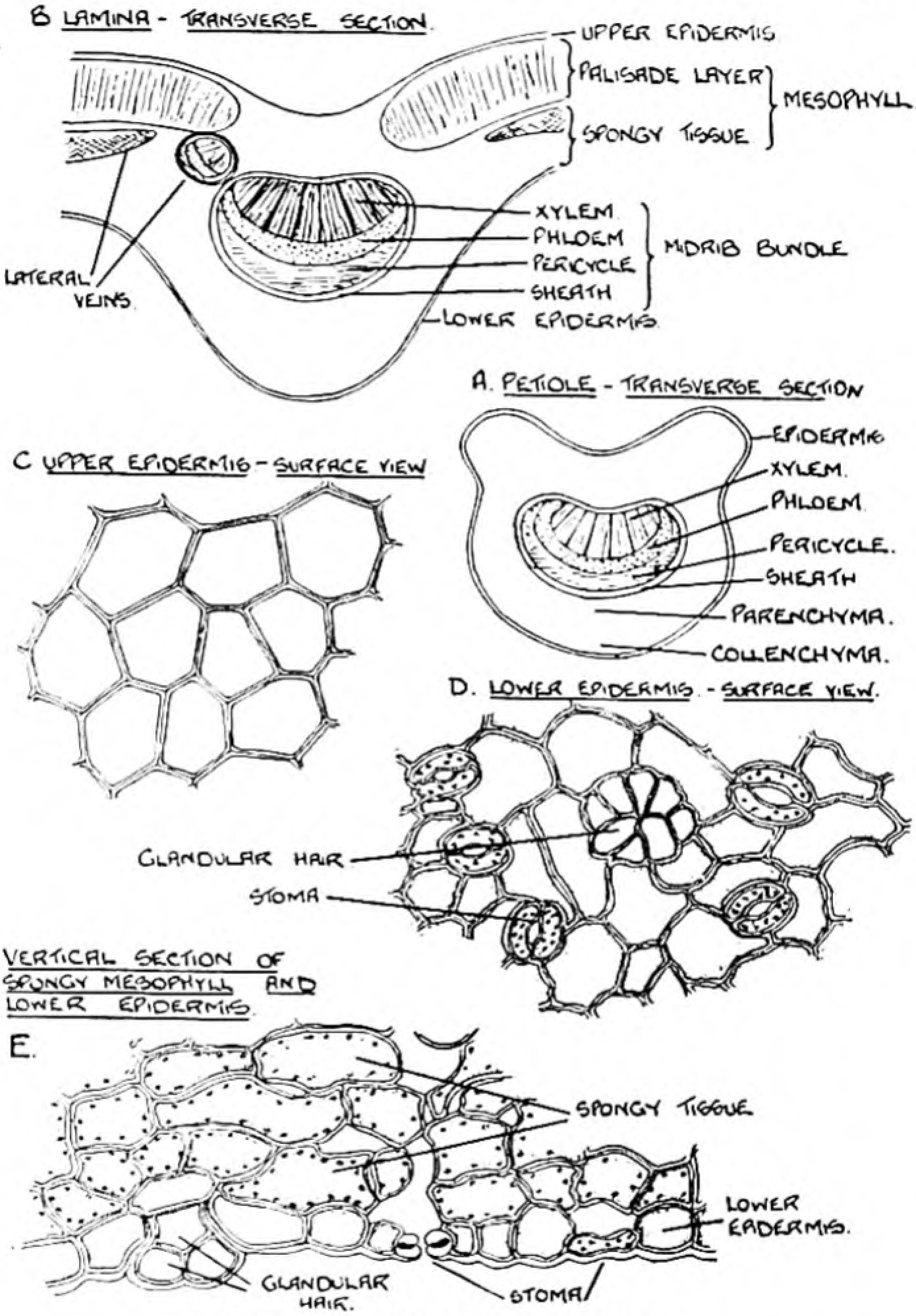

B LAMINA - TRANSVERSE SECTION.
UPPER EPIDERMIS
PALISADE LAYER
SPONGY TISSUE
MESOPHYLL
XYLEM
PHLOEM
PERICYCLE
SHEATH
MIDRIB BUNDLE
LOWER EPIDERMIS
LATERAL VEINS
A. PETIOLE - TRANSVERSE SECTION
EPIDERMIS
XYLEM.
PHLOEM
PERICYCLE.
SHEATH
PARENCHYMA.
COLLENCHYMA.
C UPPER EPIDERMIS - SURFACE VIEW
D. LOWER EPIDERMIS. - SURFACE VIEW.
GLANDULAR HAIR
STOMA
VERTICAL SECTION OF SPONGY MESOPHYLL AND LOWER EPIDERMIS.
E.
SPONGY TISSUE
LOWER EPIDERMIS.
GLANDULAR HAIR.
STOMA

Fig. 113. Leaf of Privet.

A, T.S. Petiole; B, Section across midrib region of lamina (diagram); C, Upper, D, Lower epidermis, surface view; E, V.S. Spongy mesophyll and lower epidermis.

a diagrammatic representation of the distribution of the tissues as seen in a vertical section of the lamina in the region of the midrib, and also detailed drawings. The cells of the upper and lower epidermis appear somewhat rectangular in section. They are living cells whose outer surface is covered with a cuticle. Stomata are confined to the lower epidermis and are cut in various directions by the section. Glandular hairs are also present in the lower epidermis, sunk in depressions. The **mesophyll** has an upper region consisting of about three layers of cylindrical cells whose long axes are at right angles to the epidermis. This is the palisade parenchyma. Narrow intercellular spaces run between these cells, as is shown by the imprisoned air when a section of a fresh leaf is cut and mounted in water. The lower part of the mesophyll consists of irregular cells, loosely arranged, thus leaving large intercellular spaces between them. All the intercellular spaces communicate with each other and with the stomata. The cells of the mesophyll contain numerous chloroplasts embedded in the cytoplasm lining the cell-wall. (See also Figs. 6 and 22.) The close packing of the palisade cells renders the upper surface of the leaf a darker green than the lower surface.

The palisade tissue is concerned chiefly with photosynthesis, and although the spongy tissue also discharges this function, its importance lies rather in its intercellular-space system which permits of free diffusion of gases and water vapour between the plant and its environment through the stomata. Thus carbon dioxide present in the air enters the stomata and ultimately penetrates between the palisade cells, whilst oxygen resulting from photosynthesis is able to diffuse out of the leaf through the stomata. Similarly the reverse process takes place during respiration, whilst water-vapour given off from the mesophyll cells into the intercellular spaces diffuses out through the stomata into the surrounding air.

Between the palisade and spongy mesophyll run the vascular bundles. Where a vein is cut transversely, as in the midrib, it is readily seen that the xylem is towards the upper and phloem towards the lower surface of the leaf. In a section of a reticulately veined leaf, such as privet, some veins will be cut obliquely or longitudinally. Endodermis and pericycle, although present round the larger bundles, are not easily recognisable. The endodermal cells contain small starch grains which stain with iodine solution. Hence the name starch-sheath. The pericycle is absent in the smaller veins.

Surface preparations of the upper and lower epidermis of privet leaf are illustrated in Fig. 113, C and D. The cells of the upper epidermis have straight walls and are polygonal in shape, those of the lower epidermis have curved walls and are irregular in shape. Stomata are numerous in the lower epidermis, and the discoid heads of glandular hairs are seen.

In many leaves, particularly leathery ones such as *Ficus elastica* and *Prunus Lauro-cerasus*, groups of palisade cells are seen to converge at their inner ends towards single mesophyll cells (Fig. 114).

The latter have been called collecting-cells, it being supposed that they collect the carbohydrates synthesised in the palisade cells and pass them on to the tissues of the vascular bundle.

The structure of different leaves varies considerably in detail. The palisade tissue is well developed in the leaves of plants which grow exposed to bright sunlight; it is poorly developed in shade plants. Sometimes in the same plant "sun-leaves" may be distinguished from "shade-leaves" by their thicker texture and greater development of palisade tissue. Strengthening bands of sclerenchyma may be developed, usually in relation to the vascular bundles, or at the leaf-margins. Cells containing crystals, or cavities containing oil may be present. Epidermal cells may contain mucilage as in Buchu and Senna, or be modified and serve for water-storage as in some xerophytes. In holly and india-rubber plant the epidermis may have a hypodermis of one or more layers of cells below it (Figs. 13 & 33, B).

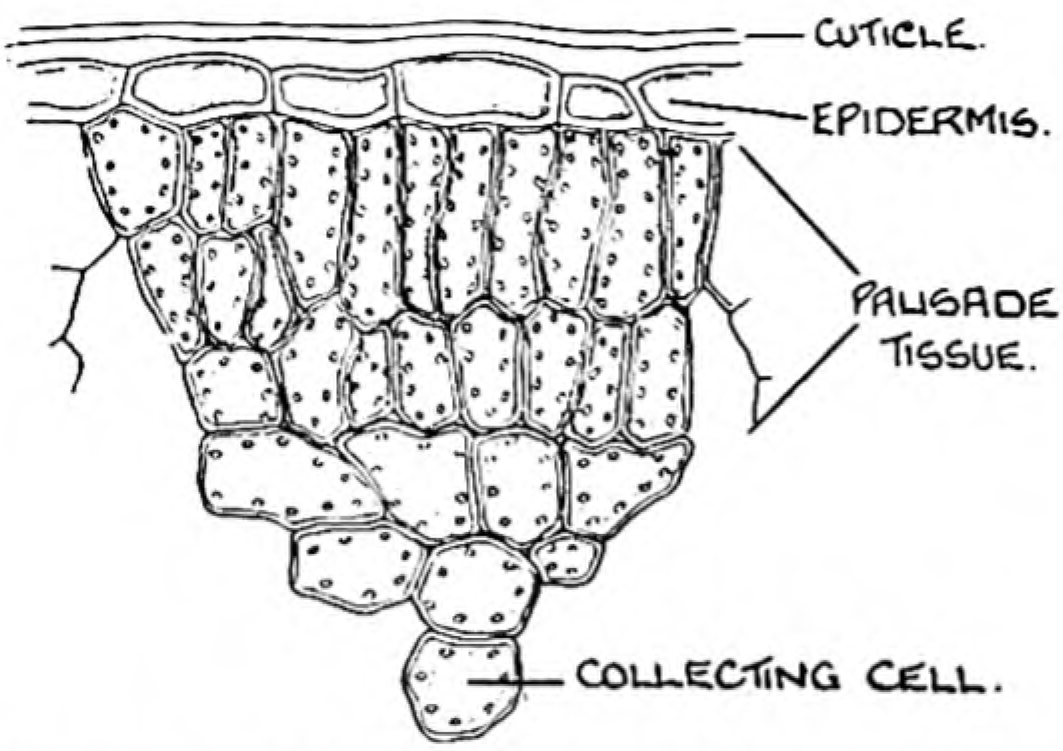


Fig. 114. ARRANGEMENT OF PALISADE CELLS IN LEAF OF *Prunus Laurocerasus* TO FORM A "COLLECTING SYSTEM."

The leaves of many Monocotyledons stand more or less erect. Here well-marked palisade tissue is absent and the mesophyll consists of small rounded cells containing chloroplasts. The vascular bundles, however, are all similarly oriented.

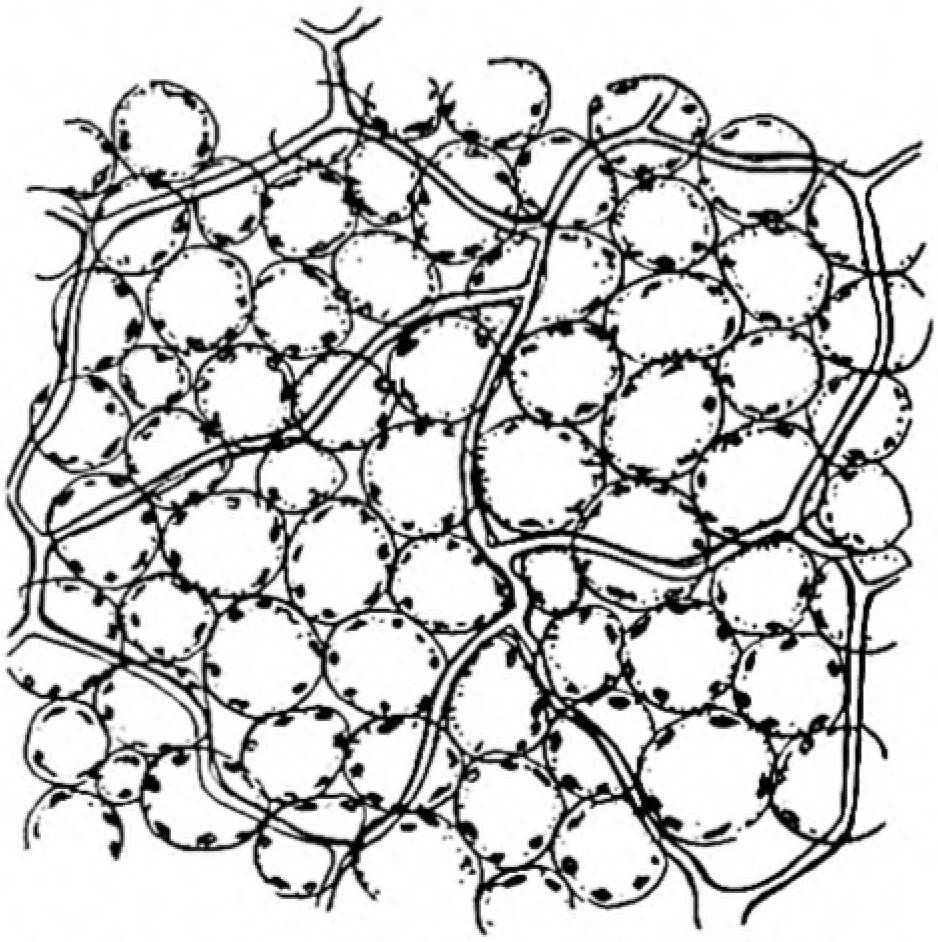


Fig. 115. PORTION OF LEAF OF *Atropa Belladonna*.

Cleared to show the palisade cells with intercellular spaces below the upper epidermis.

16. Leaf Structure by Clearing

Leaf structure may also be studied further by clearing a piece of the lamina with a reagent such as chloral hydrate or Eau de Javelle. If such preparations are examined under the microscope it is possible to see the size and shape of the epidermal cells, the distribution of the stomata and the characters of the hairs. Below the upper epidermis, the palisade cells appear circular, and the intercellular spaces between them are recognisable (Fig. 115). Cleared preparations are particularly useful for studying the structure of the smaller veins. Frequently these anastomose or fuse with others, enclosing " vein-islets " of mesophyll. Sometimes the veinlets end blindly in the mesophyll (Fig. 116); the sieve-tubes become smaller, the companion cells relatively more prominent, the larger xylem vessels give place to narrower and shorter spiral and reticulate tracheides. Finally there is no differentiation in the phloem and a short spiral tracheide terminates the xylem.

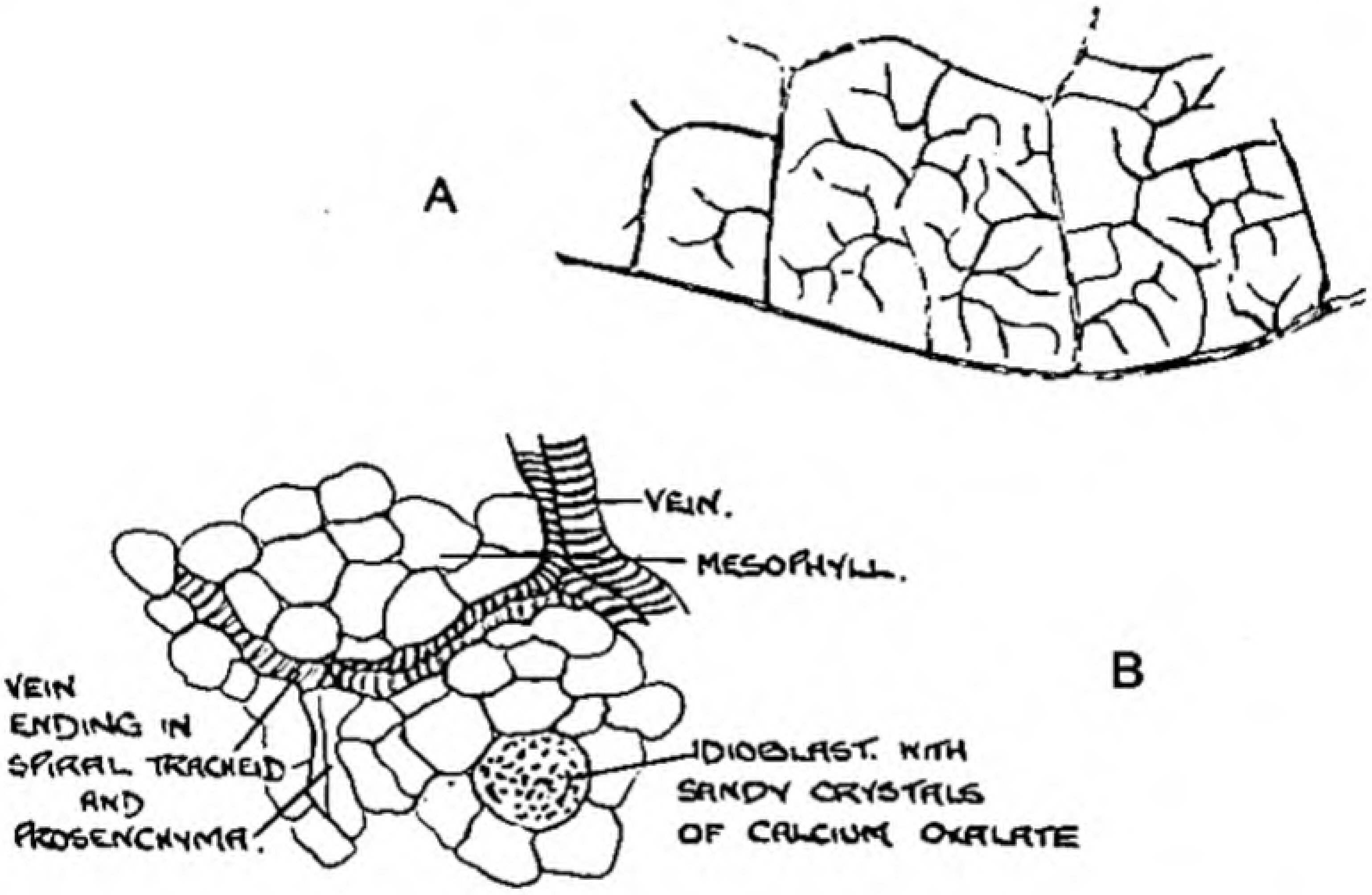

A
VEIN.
MESOPHYLL.
B
VEIN ENDING IN SPIRAL TRACHEID AND PROSENCHYMA.
IDIOBLAST WITH SANDY CRYSTALS OF CALCIUM OXALATE

Fig. 116. PORTION OF LAMINA OF *Atropa Belladonna.*

Cleared with chloral hydrate to show A, vein islets (low power view) and B, vein ending (high power).

Sometimes the vein-endings near the margin of the leaf are in close association with the small-celled glandular tissue, of hydathodes (see Fig. 28). The epidermis in contact with each hydathode has one or more water-pores (Fig. 37). These are usually larger than ordinary stomata, and their guard-cells have lost the power to control the size of the aperture, so that the pore remains permanently open. Water-pores are found at the tips of leaves of grasses, and on the margins of a number of dicotyledonous leaves (e.g. *Digitalis, Lobelia, Saxifraga* species) associated with hydathodes.

Chloral hydrate dissolves out the cell contents such as protoplasm and starch, but does not destroy calcium oxalate crystals. Hence the characters of the latter can be studied in carefully cleared preparations.

17. Isobilateral and Centric Leaves

In the isobilateral leaf of *Iris* the mesophyll presents the same appearance towards both surfaces. In a transverse section of the lower, sheathing part of the leaf there are two series of bundles, one towards each side, the phloem portions of the bundles in each series being directed outwards towards the epidermis. In the narrower upper region the bundles lie more or less in the same plane, some with xylem directed one way, others with it pointing the opposite way.

In centric leaves, e.g. onion, there is a radial arrangement of tissue.

18. Development of the Leaf Structure

The development of the stem-apex, including the young leaves has already been described (p. 49, and Fig. 32). At first all the cells of the developing leaf are meristematic, but later the meristematic tissue is restricted to the middle or base, and growth is therefore *intercalary*. Finally, when the full number of cells has been produced, meristematic activity ceases. At this stage the young leaf is still very small and folded up in the bud with the other leaves. The expansion and increase in size of the leaf, when the bud unfolds, is due to the extension-growth of the individual cells, not to the formation of new cells.

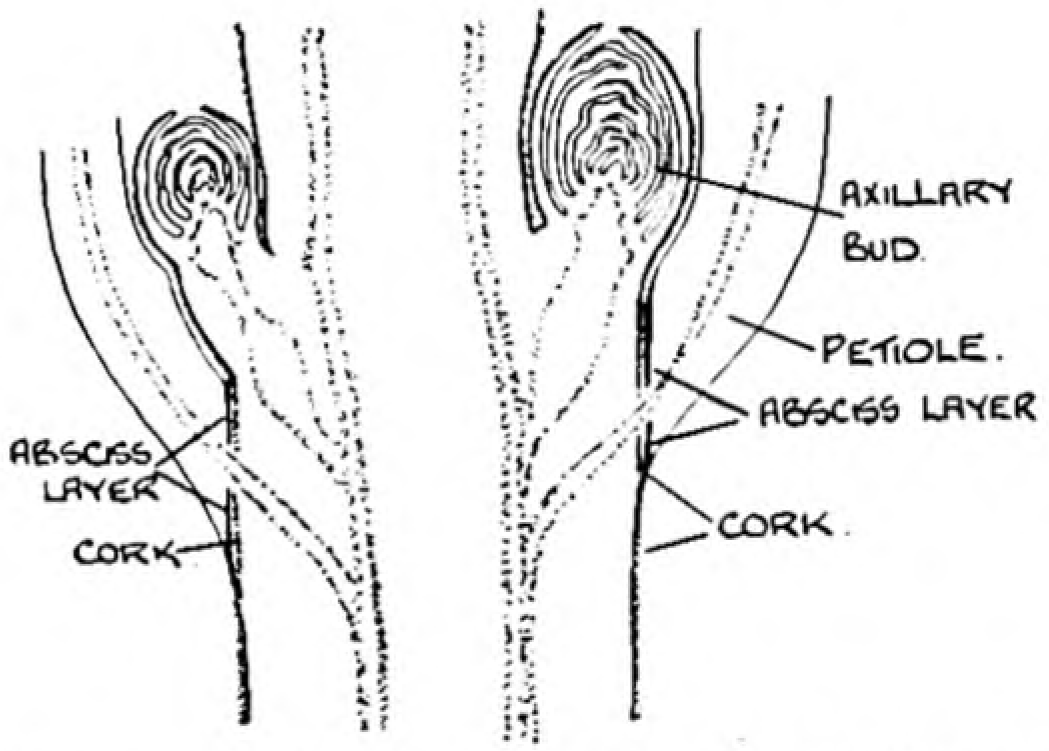


Fig. 117. L.S. Node of *Acer pseudoplatanus* showing Preparation for Leaf-fall.

19. Leaf-fall

Leaf-fall is a periodic phenomenon which follows the formation of an *absciss layer* at the base of the petiole. In deciduous trees, which lose their leaves on the approach of winter or with the onset of a dry season, leaf-fall is clearly related to seasonal climatic conditions, but evergreens may shed their leaves at other seasons, as in the spring. Further, tropical trees shed their leaves periodically, even in the absence of pronounced changes in temperature. The *causes* leading to leaf-fall are not clearly understood, but the shedding of leaves can be induced sometimes by exposure to dry conditions or to toxic gases. It is important to realise that leaf-fall is a *vital* phenomenon which follows the special metabolism of cells at the base of the petiole. Strong winds only cause the fall of the leaves whose connexion with the parent stem has been already almost severed by the formation of an *absciss layer*. The leaves on dead branches do not fall. They wither, but no absciss layer is formed, and so they are not shed.

The absciss layer is formed by a plate of parenchymatous cells containing dense protoplasm close to the base of the petiole. These cells round off and at the same time chemical changes take place in their cell-walls which render the middle lamellae mucilaginous. They are thus readily separable, so that the leaf ultimately is held in position only by its vascular strands. These are eventually broken by the weight of the leaf and by the action of wind and frost. The leaf-scar thus exposed is protected either by changes taking place in the cell-walls of cells below the absciss layer, or by the formation of cork cells from a phellogen, the periderm thus produced in time becoming continuous with that of the stem. (Fig. 117.)

The casting of small branches commonly observed in forest trees especially in dry seasons, and of flowers, inflorescences and fruits, is a similar process, resulting from the formation of absciss layers at their bases.

CHAPTER VII

NUTRITION AND GROWTH

A. NUTRITION

1. We have already (pp. 8-13) mentioned certain of the physiological processes connected with the nutrition of a green plant. We shall now treat these processes in greater detail, and although they will be considered mainly with special reference to the Angiosperms, they are essentially the same in all green land plants which show the characteristic differentiation into root, stem and leaf.

2. Importance of Water

Water is always present in living plant tissue. In many fruits water may constitute 90 per cent. or even more of the total weight, whilst in green foliage-leaves the content of water is sometimes as high as 80 per cent. Even "dry" seeds contain an appreciable amount of water, frequently from 10 to 12 per cent. The importance of a full supply of water is clearly demonstrated by the behaviour of many seeds. Seeds of the garden pea (*Pisum sativum*) or broad bean (*Vicia faba*) will remain "dormant" for many months if they are in a "dry" condition. When they are soaked in water they rapidly absorb the water. Within 24 hours their weight may have doubled. They begin to germinate and become active only when they have absorbed water. Even in the "dry" state they are not completely "dormant." Certain vital activities such as respiration are proceeding but only at a very low rate. These metabolic processes are speeded up enormously when the water content of the seeds increases.

Water, too, is required by the plant to make good the losses of water by transpiration. When the atmosphere is at all dry the leaves are continually losing water by transpiration, and unless this water is replaced the cells of the leaf lose their turgidity and the leaf wilts. This phenomenon is readily seen in the case of cut shoots, in which the leaves continue to lose a certain amount of water which they are unable to replace.

3. The Food Materials of a Green Plant

If we make a chemical analysis of a plant—an analysis of the gases given off, and the residue or *ash* left behind on burning the plant—we find appreciable amounts of the following chemical elements: carbon, oxygen, hydrogen, nitrogen, sulphur, phosphorus, calcium, potassium, magnesium, sodium, and chlorine, small amounts of iron and silicon, and frequently, traces of manganese, iodine, boron, zinc, copper, and many others. Of these probably only the first six enter into the composition of the living substance (*i.e.* the protoplasm) of the plant. It is evident that all these elements must be present in the food-materials of the plant, and we have already indicated that the food-materials absorbed by a green plant consist of simple inorganic substances which must be presented to the plant in the form of a solution.

All the carbon of the plant (and the dry matter of the plant contains about 40 per cent. of carbon) is derived from the carbon dioxide of the atmosphere, which is absorbed by the green parts of the plant. All the other elements found in plant material are derived from the water and dissolved mineral substances that have been absorbed by the roots. The oxygen and hydrogen present in the plant are derived chiefly from the water that has been absorbed in this way.

4. Osmosis and Osmotic Pressure

Let us consider an experiment set up as in Fig. 118, B. A hollow cylinder of parchment or collodion is closed at the lower end with a rubber bung, whilst the top of the cylinder is fitted with a stopper carrying a vertical glass tube. The parchment membrane is so prepared that it is permeable to water, but impermeable to sucrose, *i.e.* it is semipermeable.* The parchment cylinder is filled with a concentrated sucrose solution and immersed in water. Immediately water will begin to move through the parchment membrane into the interior of the cylinder. The volume of liquid in the cylinder therefore increases and so the level of the liquid in the vertical glass tube rises. This diffusion of water is termed *osmosis*. As this process goes on the level of the liquid in the vertical tube continues to rise, and this column of liquid exerts a downward pressure tending to force water molecules out of the cylinder through the membrane. The **osmotic pressure** of the solution is the force holding up this column of liquid. Finally a state of equilibrium is reached when the movement of water into the cylinder exactly equals the outward movement, and the level of the liquid in the vertical tube undergoes no further change. It is clear that at this point the osmotic pressure of the solution equals the downward pressure of the vertical column of liquid in the glass tube. The osmotic pressure of a solution depends primarily on its concentration. A molar solution of sucrose, for example, we may assume exerts an osmotic pressure of 22·4 atmospheres.

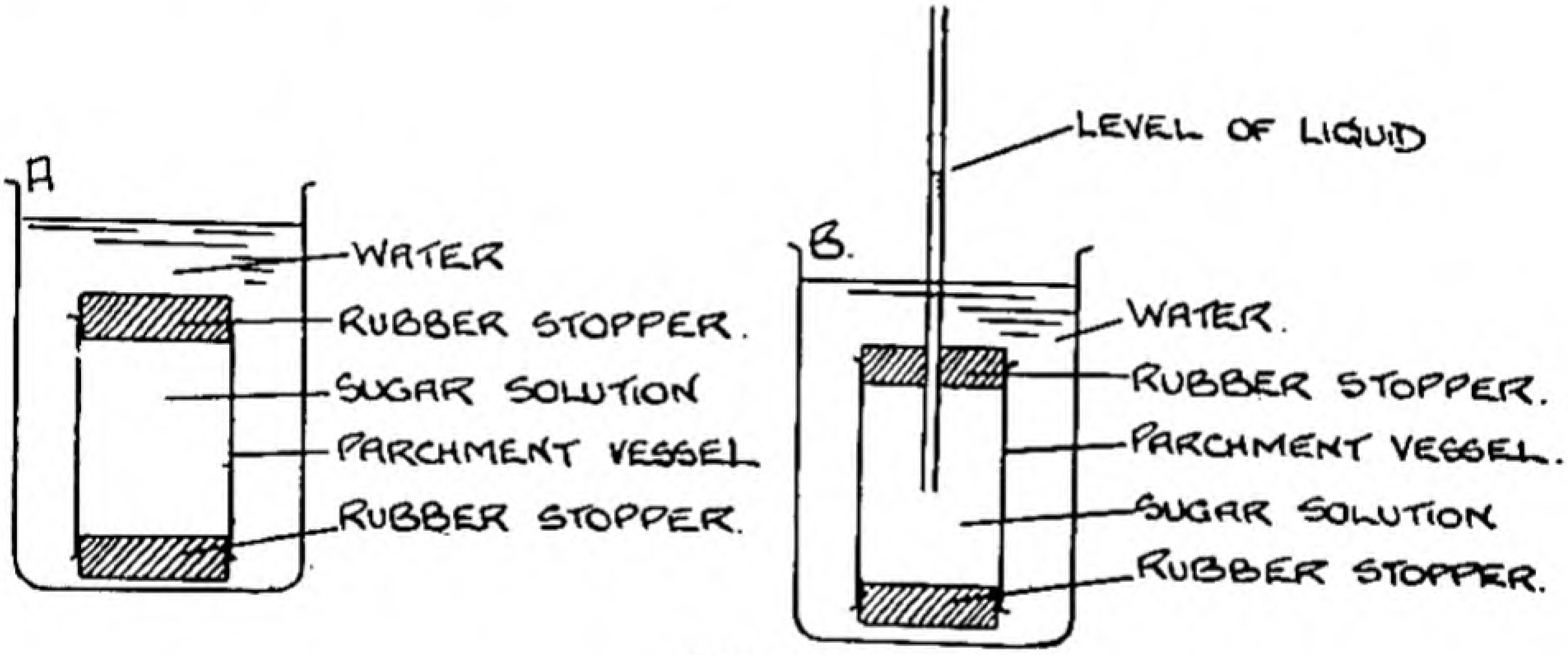


Fig. 118.

A, Parchment cylinder: Osmosis. B, Parchment cylinder with Manometer.

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[*] A semipermeable membrane is one which is permeable to (*i.e.* allows the passage of) a solvent but is impermeable to a solute. The membrane may be permeable to one solvent and not to another or impermeable to one solute and permeable to another. Strict accuracy therefore demands that we should say that a membrane is semipermeable to certain solvents and solutes. In plant physiology we are almost invariably dealing with aqueous solutions, and when we speak of a semipermeable membrane we mean one permeable to water and impermeable to the substances dissolved in that water.

We might have arranged the apparatus shown in Fig. 118, B, rather differently, using a parchment cylinder closed at both ends with rubber stoppers. If such a cylinder (Fig. 118, A) filled with sucrose solution were immersed in water, the cylinder would soon become distended, due to the passage into it of water by osmosis. The distended walls of the cylinder would now be pressing inwards, *i.e.* exerting an inward pressure. At equilibrium this inward pressure of the cylinder walls would exactly equal the osmotic pressure of the sucrose solution contained within the cylinder. At this point water is moving across the membrane at equal rates in both directions, and so the net movement is nil.

If instead of surrounding the cylinder with water we had immersed it in a weak sucrose solution, water would still have entered the cylinder by osmosis. An important general rule to remember is that when two solutions of different concentrations are separated from each other by a membrane permeable to the solvent (in this case water), and impermeable to the solute (in this case sucrose), water will pass through the membrane from the weaker to the stronger solution.

5. Osmotic Relations of a Plant Cell

The normal vacuolated plant cell consists of a vacuole, surrounded by at least two membranes: the cytoplasm and the cellulose cell-wall (Fig. 10). The cytoplasm with its surface layers more or less sharply differentiated may itself constitute more than a single membrane. The vacuole of the cell contains the cell-sap, which is an aqueous solution of organic and inorganic substances, and with an osmotic pressure. Direct measurements on the sap expressed from plant cells show that the cell-sap commonly has an osmotic pressure of from five to twenty-five atmospheres, but in exceptional cases it may be over one hundred atmospheres.

In plant cells the cellulose cell-wall does not function as a semipermeable membrane. Water and dissolved substances pass through it freely. The layer of living cytoplasm which lines the cell-wall internally is, on the other hand, a semipermeable membrane so far as most solutes are concerned. The semipermeable properties of the cytoplasm depend on the fact that it is alive. When killed it becomes permeable to dissolved substances. This is readily demonstrated with cubes of beetroot. If small cubes of beetroot are prepared, washed to remove the red pigment from the damaged superficial cells of the cubes, and then immersed in water, no pigment will diffuse out from the cells into the surrounding water. It is retained in the vacuoles of the cells by the action of the semipermeable living cytoplasm. A similar set of cubes of beetroot, washed and then immersed in boiling water, or in alcohol, which kills the cytoplasm, soon colour the surrounding liquid. The dead cytoplasm is permeable, and so the red pigment diffuses freely out of the cells.

The vacuolated cell, then, consists of a vacuole containing a solution with an osmotic pressure, surrounded by a semipermeable membrane, the cytoplasm, the whole being contained within a permeable cellulose cell-wall. If such a cell is immersed in water we have a relatively strong solution (the cell-sap) separated from an infinitely weak one (water) by a semipermeable membrane (the cytoplasm). Under such conditions water will pass from the weak to the strong solution by osmosis. Thus water will pass into the vacuole of the cell by osmosis, or in other words, the cell will absorb water.

The whole of the osmotic pressure of the cell-sap may not be available for absorbing water. If we take the case of a cell whose cell-sap has an osmotic pressure of 12 atmospheres placed in a solution also with an osmotic pressure of 12 atmospheres, no water-absorption will take place. If the same cell is placed in water (with an osmotic pressure *nil*) the whole of the osmotic pressure of the cell-sap is drawing water into the cell. This available osmotic pressure, which is the difference between the osmotic pressures of the cell-sap and the external solution, is known as the *suction force.* The cell-wall is slightly extensible, and as water passes into the cell and the volume of the vacuole increases, a pressure is exerted on the cell-wall and finally equilibrium is established. The increase in the volume of the vacuole and the consequent dilution of the cell-sap is small and so the osmotic pressure only falls slightly, say to 11 atmospheres. The cell is now fully distended and hence can absorb no more water, although there is a difference of 11 atmospheres between the osmotic pressures of the internal and external solutions. The whole of this difference, however, is used in stretching the cell-wall and keeping the cell turgid. The pressure exerted on and stretching the cell-wall is known as *turgor pressure.* This is exactly counterbalanced by the inward pressure of the stretched cell-wall, known as the *elastic pressure* of the cell-wall. Hence the force available for drawing water into the cell is not the osmotic pressure of the cell-sap, nor even the difference between the osmotic pressures of the internal and external solutions, but it is this difference less the turgor pressure. Therefore Suction force = (Osmotic pressure of cell-sap − Osmotic pressure of external solution) − Turgor pressure. The osmotic pressure of the cell-sap indicates the maximum possible suction force exerted only when the cell is flaccid (*i.e.* turgor pressure *nil*) and immersed in water.

So far we have considered the behaviour of a plant cell when it is immersed in a solution whose osmotic pressure is less than that of the cell-sap. If, however, we place the cell in a solution more concentrated than the cell-sap, water will be withdrawn from the vacuole. This osmotic withdrawal of water from the cell is called exosmosis, whereas the osmotic absorption of water is frequently termed endosmosis. When the cell is immersed in concentrated salt solution the solution diffuses freely through the cell-wall and so comes into contact with the cytoplasm of the cell. Osmotic withdrawal of water from the vacuole occurs, the volume of the vacuole decreases and the cytoplasm is no longer pressed against the cell-wall, but contracts away from it, and may form a more or less spherical mass still enclosing the shrunken vacuole (Fig. 119). The space between the cell-wall and cytoplasm is filled by salt solution. This phenomenon is known as plasmolysis. If such a plasmolysed cell is placed in water, it absorbs water osmotically. The semipermeable properties of the cytoplasm are unimpaired and the cell becomes turgid again.* Manifestly a solution with an osmotic pressure greater than that of the cell-sap will bring about plasmolysis, and hence we can obtain an estimate of the osmotic pressure of the cell-sap by finding the maximum concentration of external solution which just fails to cause plasmolysis.

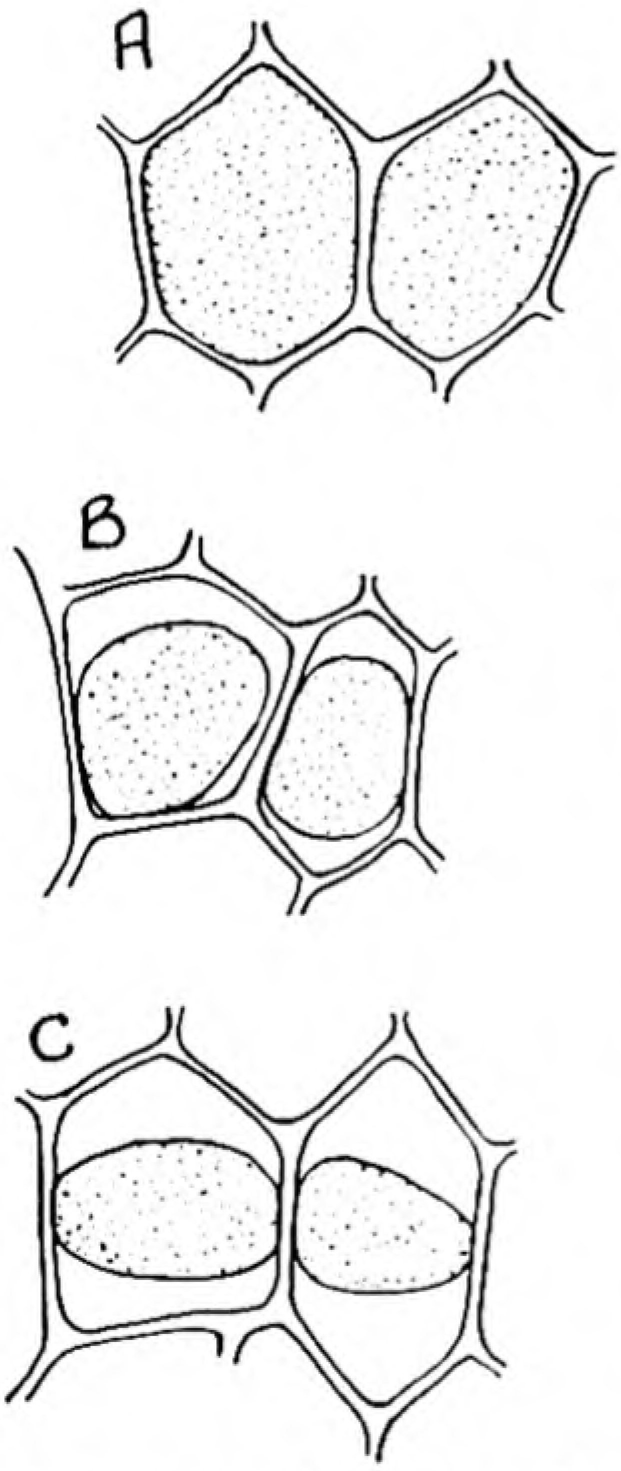

Fig. 119. PLASMOLYSIS.

6. Absorption of Water by Roots

The root-hairs are found only in a very restricted region of the root near, but not actually at, the tip of the root (see Fig. 90). Water absorption by the root is confined to this zone. Ordinarily the length of a root-hair is from 0·5 to 3·0 mm. (*i.e.* much longer than the normal plant cell), and as there may be several hundred root-hairs on a single square millimetre of the root, their presence brings about a very large increase in the absorbing area of the root and helps to render a thorough exploitation of the soil possible. The root-hairs come into close contact with soil-particles, each of which is surrounded with a film of soil-water, *i.e.* a *very weak* solution of mineral salts. Inside the hairs is the cell-sap, a *comparatively* strong solution of sugars, organic acids, etc. The permeable cellulose wall of the root-hair is lined inside with the layer of living cytoplasm, which forms a semipermeable membrane on the inside of the cellulose wall, and it is this membrane which controls the osmotic intake of water from the soil. Thus water is absorbed from the soil solution by osmosis. This process of water absorption is greatly accelerated by a rise in temperature.

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* If, in plasmolysing a cell, the protoplasm shrinks to a spherical mass as described above, the protoplasmic connexions through the cell-wall are broken, and even if it recovers its turgidity on bathing it in water, to this extent the cell is damaged.

7. The Soil

Soils owe their formation mainly to the weathering of rocks. The two main weathering agents are frost, and water containing carbon dioxide in solution. As a result of this disintegration of the rocks mineral particles of various sizes are formed, and these constitute the mineral skeleton of the soil. The sizes of the mineral particles of the soil depend on many factors, such as the type of parent material, mode and degree of weathering and on whether the soils have been formed *in situ* or transported either by wind or water from the place of weathering and deposited elsewhere. The climatic conditions under which the soil has been formed exert a great influence on the soil type. Especially is the rainfall important as this determines to a great extent the loss of certain soil constituents by drainage.

The soil does not consist entirely of mineral particles. Organic matter both of animal and vegetable origin, and in varying stages of decomposition, is present, except in a few soils such as freshly deposited sand. The organic matter, together with certain inorganic substances, helps to cement the ultimate mineral particles of the soil into larger aggregates, thus giving the soil its typical crumb structure. To this many of its properties are due. The organic matter of the soil, partially decayed and called **humus**, is important too, because of its marked colloidal properties, which confer on the soil the power of absorbing and holding water. Mineral substances, also, especially bases, are adsorbed by the colloidal humus and thereby prevented from being washed out of the soil. The humus serves as a food substance for many of the micro-organisms found in the soil. The soil atmosphere, which largely fills the spaces between the soil particles, is not identical with normal air. It is commonly richer in carbon dioxide, due chiefly to the respiration of the soil flora (Fungi, Bacteria and Algae) and the soil fauna.

8. Soil Water

When a soil is flooded with water and then allowed to drain, some of this water drains away under the influence of gravity. This is the gravitational water. Most of the water that remains is capillary water and forms films, which are held by surface tension forces, around the soil particles. This capillary water is of great importance to the plant. There is also in the soil a certain amount of hygroscopic water, water imbibed by the soil colloids, or present as water of crystallisation. The three fractions—gravitational water, capillary water and hygroscopic water are not sharply defined. The capillary water is the most important so far as the plant is concerned and its amount is determined by the thickness of the film of water surrounding the soil particles and by the size of the particles. The total surface of the soil particles increases rapidly as the size of the individual particles decreases. Consequently the smaller the particles the greater the water capacity of the soil.

The determination of the size of the soil particles is therefore the first step in soil analysis. After removal of the stones and gravel by sieving, the soil is dispersed in water and the soil particles fractionated by sedimentation. These are separated into four classes, namely, coarse sand, fine sand, silt and clay, with the limits of particle diameter 0·2–2·0 mm., 0·02–0·2 mm., 0·002–0·02 mm., and less than 0·002 mm. respectively. The terms sand and clay are used here to indicate soil particle size only and do not imply that these particles consist of pure silica or alumina.

Soils in which coarse particles (e.g. sand) predominate are called sandy or light, and are easy to cultivate. Because of the large particles which pack loosely they drain readily. On the other hand the lack of fine colloidal particles means that nutrients are easily washed out of the soil. Heavy clay soils contain a preponderance of fine clay particles. These may, however, be aggregated in such a way that large " clods " are produced. The abundance of fine colloidal particles increases the water-holding capacity of the soil, prevents the loss of basic substances by drainage, and impedes the drainage of the soil, whilst the peculiar physical condition of the clay may result in the soil forming a pasty intractable mass under certain conditions. The physical properties of both heavy and light soils are considerably modified by the presence of humus and of calcareous matter. Clay soils are rendered much less intractable and more friable by calcium compounds. Decaying organic matter (humus) renders heavy clay soils more open in texture, and improves the water-holding capacity of sandy soils because of its colloidal properties.

When a soil has drained to such an extent that there is no gravitational water present, the water films around the soil particles are relatively thick. The root-hairs of the plant are in contact with these soil particles, and water passes into the root-hairs by osmosis. As water absorption proceeds, the water films around the particles become much thinner, and this water is then held more tenaciously by the soil particles. Finally a point is reached when the remaining water of the soil is held so tenaciously that water absorption by the root-hairs ceases, in spite of the fact that the osmotic pressure of this soil "water" (really a dilute solution) is much lower than that of the cell-sap in the vacuole of the root-hair. The amount of this non-available water will vary according to the size and nature of the soil particles. It is greatest, and may reach a value of 16 per cent. of air-dry soil, with clay soils where fine colloidal particles are abundant. It may be as low as 3 per cent. for sandy soils.

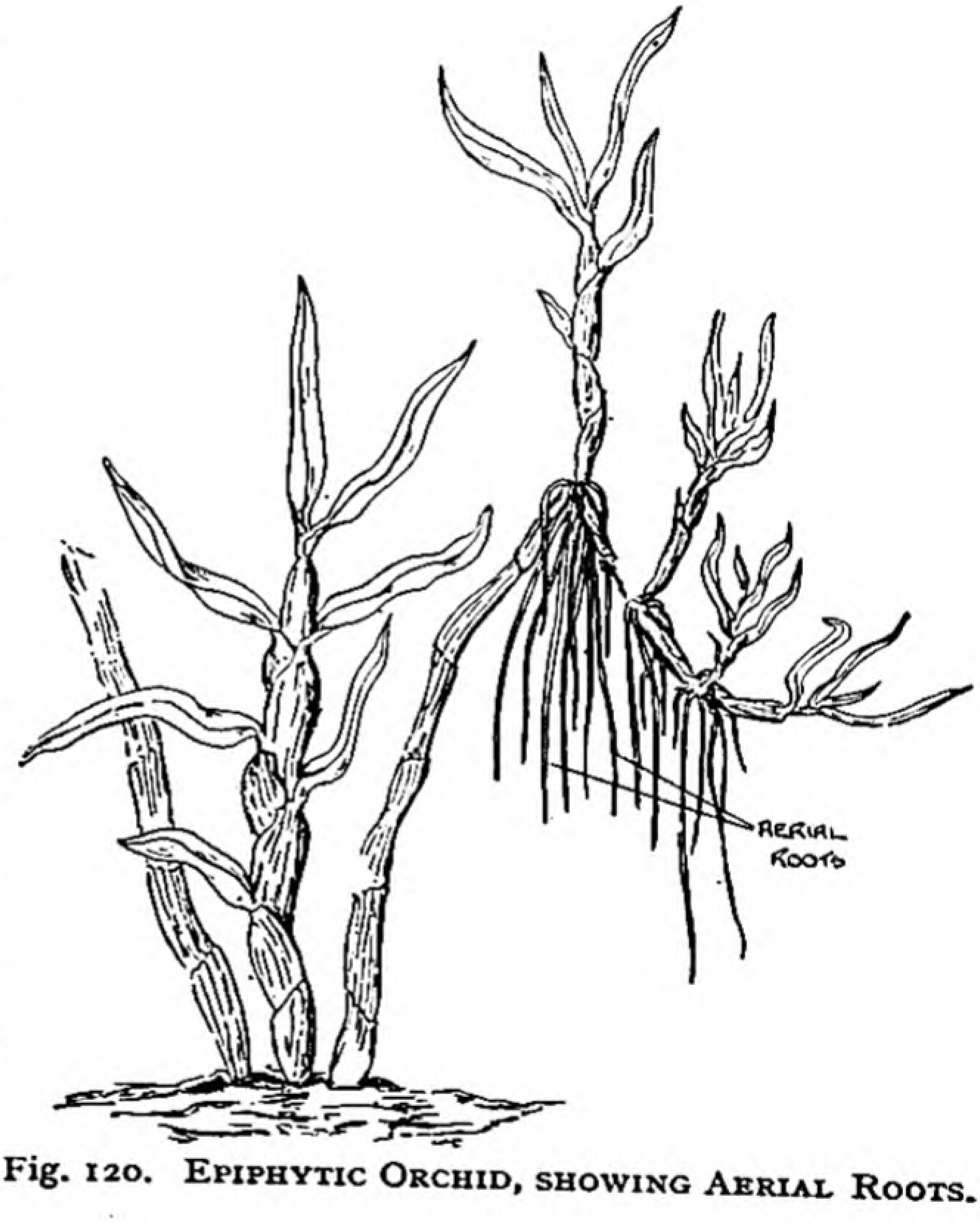


Fig. 120. EPIPHYTIC ORCHID, SHOWING AERIAL ROOTS.

9. Exceptional Methods of Water Absorption

Many epiphytic plants, which have no connexion with the soil, possess special means of absorbing water. They often develop **aerial roots** (Fig. 120). These are adventitious roots which hang down into the air from the plants which are growing lodged on the trunks and branches of trees. In these roots the water absorption is carried on by a special tissue—the velamen. In transverse section (Fig. 121) such a root is seen to possess a normal central stele surrounded by the cortex. Between stele and cortex, there is an endodermis like that described for monocotyledonous roots (Fig. 93). The outermost layer of the cortex is specialised to form an exodermis in which the outer and lateral walls are thickened, except in certain passage cells which remain thin-walled. External to the exodermis is the velamen, a mass of tissue several cells thick and consisting of empty cells with thick spiral strands on their walls. These cells are able to absorb water like a sponge. Rarely, a velamen occurs on earth roots, being found, for instance, on the roots of *Clivia nobilis*. Other epiphytic plants possess special water-absorbing hairs. They are extensively developed in *Tillandsia usneoides* (Spanish moss) and the bulk of the water requirements of this plant are satisfied by the water absorbed by these special hairs. It is important, too, to realise that the leaves of most land plants can absorb water when they are wetted, but the proportion of their total water requirements obtained in this way is very small.

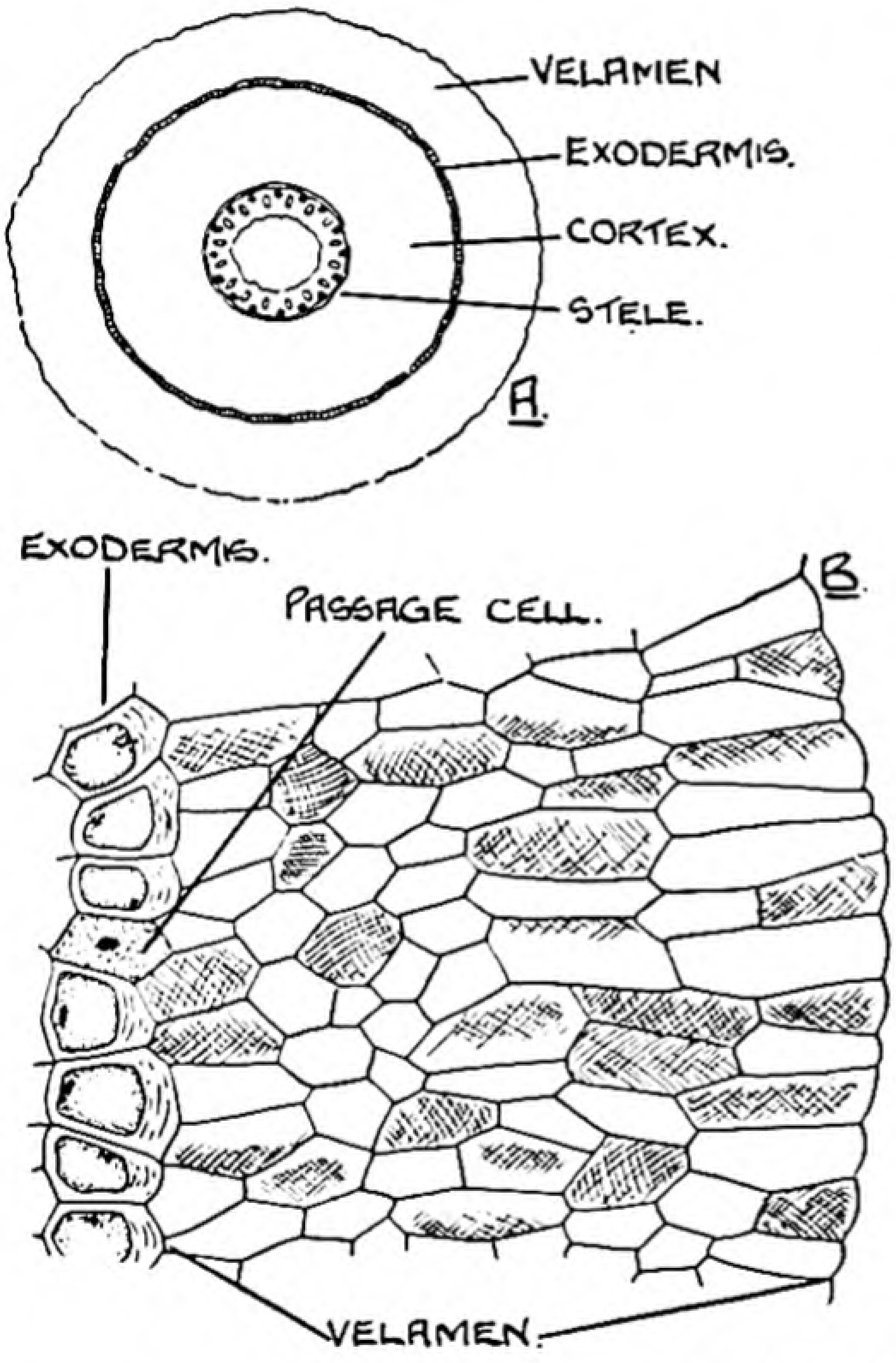


Fig. 121. Epiphytic Orchid, Transverse Section, Aerial Root.

10. Course of the Absorbed Water

We have already indicated that water enters the plant through the root-hairs. Most of the water absorbed in this way is finally lost from the aerial parts of the plant (especially the leaves) in the process of transpiration. We have therefore to trace the path of the water from the root-hairs to the foliage leaves. Reference to Figs. 92 and 93 will show that in the absorbing region of the root we have root-hairs in contact with the soil externally, and with the cortical cells internally, and we can represent the structure of the root at this point diagrammatically as in Fig. 122.

Here A represents the cell of the piliferous layer bearing a root-hair; B to H are cortical cells, I the endodermis, J the pericycle and K a xylem vessel. We have already pointed out that the osmotic entry of water into the cell is governed by the suction force exerted by the cell, and if in such an arrangement of cells there is a suitable gradient of suction force, water will enter the root-hairs, pass through the cortical cells, the endodermis and the pericycle, and enter the xylem vessel. This will occur if the suction force of A is great enough to allow it to absorb water from the soil, but is less than that of B, which, in turn, is less than that of C, and so on. The suction force of the cells B to J need not be of any great magnitude. When A absorbs water and becomes turgid it will exert no suction force and hence will readily give up water to cell B. This in turn attains a turgid condition and so cell C readily absorbs water from it. In the xylem vessel K, the whole of the osmotic pressure of the vessel contents constitutes the suction force, and hence so long as the osmotic pressure of the contents of K exceeds the osmotic pressure of the soil-water, a suitable suction force gradient can be maintained, and water will continue to pass from the soil to the xylem across the intervening cells. Water does not pass into the root cells merely to equalise the suction force of the living cells, but is actually passed into the non-living xylem elements and may be forced some considerable distance up the vessels and tracheides of the xylem into the stem. This pressure, forcing water up the stem in this way, is known as **root pressure**, a process which we shall consider later.

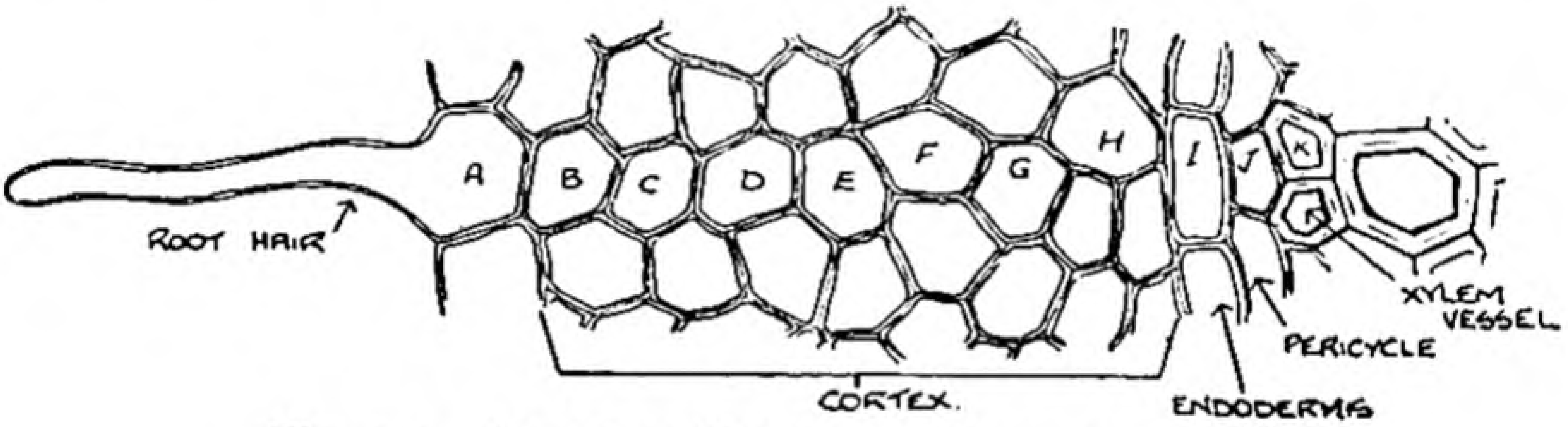


Fig. 122. DIAGRAM T.S. ROOT, GRADIENT A—K.

That the water which is passed from the living cells of the root to the xylem is transported up the stem in the non-living elements of the xylem can be demonstrated in a number of ways. By ringing experiments in which a ring of the outer tissues of the stem is removed, leaving a zone in which only the tissues internal to the cambium, *i.e.* the xylem and the pith, remain (Fig. 123), it can be shown that the upward movement of water in the stem takes place in one or the other of these tissues. This conclusion is reached because in a plant ringed in this manner sufficient water reaches the leaves to keep them turgid and healthy. A similar conclusion is reached from experiments in which a cut shoot is placed with its lower end in eosin solution. The solution is absorbed by the shoot and the eosin stains the walls of the xylem vessels and tracheides, indicating that they and not the pith or even the living cells of the vascular bundles, are the water-conducting elements of the stem. Structurally the vessels and tracheides are well fitted for this function. They have no protoplasm and vessels at least have few if any transverse septa, and so they offer relatively little resistance to water transport. Vessels with their greater diameter and length, form, as one would expect, more efficient conducting channels than tracheides. Experiments show that the ease with which water moves through the xylem is greatest when the vessels are numerous and large (as in willow and oak) and least when the xylem contains many fibres, or consists mainly of tracheides (as in larch and yew).

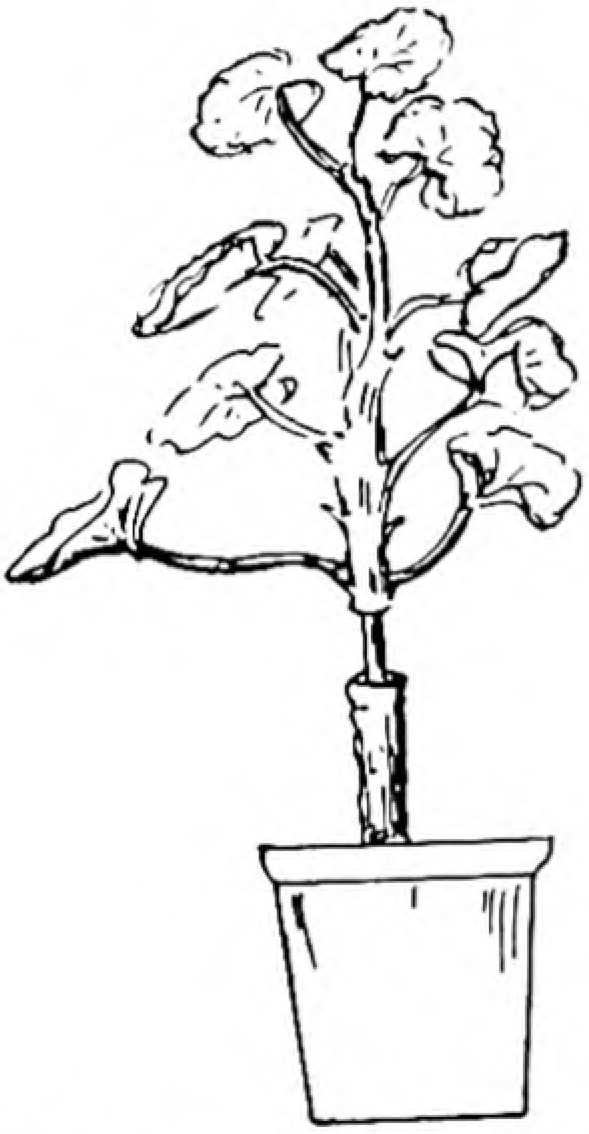


Fig. 123. Ringed Stem Experiment.

11. Transpiration

The cells of the leaf are saturated with water and are exposed to air which is more or less dry. In these circumstances the cells give up water in the form of water-vapour to the atmosphere. This loss of water is **transpiration.** The existence of this process can easily be shown by the use of a potted plant. The soil in the pot is well watered and the pot then covered with rubber sheeting to prevent loss of water by evaporation and placed under a bell-jar, and in a short time the inner surface of the bell-jar will be covered with a deposit of dew. In the absence of violent temperature fluctuations this water can have come only from the aerial parts of the plant.

The amount of water lost in the above process may be conveniently estimated by the use of the same potted plant, which should be weighed at the beginning and end of a period of say 2 hours. The loss in weight during this time gives a measure of the amount of water transpired by the plant. The possible gain in weight by photosynthesis during the period of the experiment is so small in relation to the transpiration losses that it can be neglected.

Using the same plant the amount of transpiration may be determined after both surfaces of all the leaves have been covered with a thin film of vaseline. In this case we shall find that the transpiration rate is reduced to a small fraction of its previous value. Hence transpiration occurs mainly from the leaf surfaces and only to a small extent from the surface of the stem.

Experiments of the sort described show that a surprisingly large amount of water may be given off in transpiration. A plant of *Zea mays* (maize) during its life of about twenty-six weeks may transpire over twenty pounds of water. In order to institute comparisons between the transpiration rates of different plants the transpiration is conveniently expressed as grams of water lost per hour per square metre of leaf surface.

Although transpiration involves the loss of water-vapour from the leaf it is not a simple process of evaporation. The leaf is protected from free uncontrolled evaporation by the development of a cuticle, and loss of water by transpiration occurs mainly through the stomata. This conclusion is reached as a result of comparing transpiration rates and stomatal frequencies on the two surfaces of a leaf. If, for instance, we take a series of ivy leaves and suspend them in the air of the laboratory after greasing one or both surfaces of the leaf, we find that whereas leaves with the lower surface greased remain fresh for a considerable time, those with only the upper surface greased wither rapidly, due to loss of water. The greasing of the lower side of the leaf blocks the stomatal pores, which are almost entirely confined to this surface, and hence transpiration through the stomata ceases. Alternatively, we might have fixed pieces of dry cobalt chloride paper, protected from the atmosphere, on the surfaces of the leaves. A rapid change in the colour of the paper from blue to pink indicates the liberation of water-vapour from the leaf surface. The rapidity

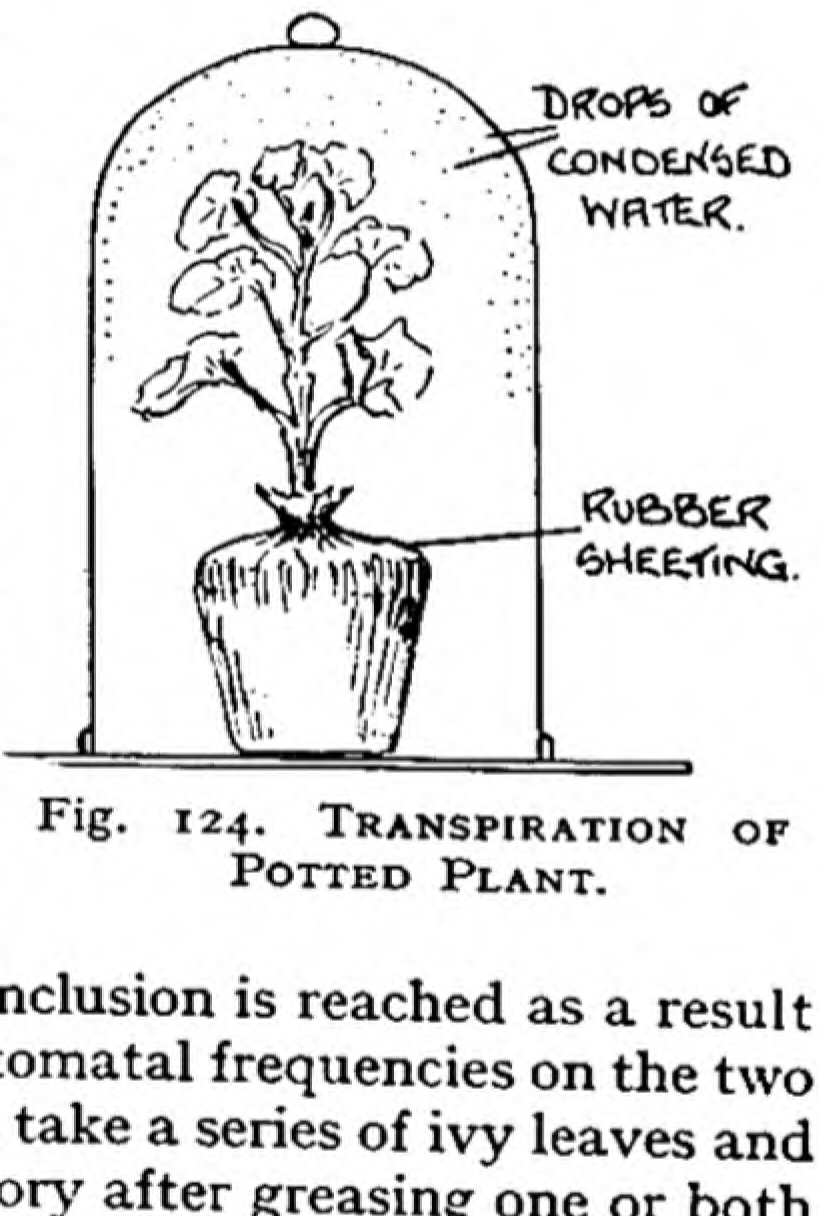


Fig. 124. TRANSPIRATION OF POTTED PLANT.

of the colour change gives a measure of the relative rates of water loss. By such methods we find that the rate of transpiration is greatest from the surface where the stomata are most abundant.

Hence with most dorsiventral leaves transpiration occurs mainly from the lower side of the leaf where the stomata are most numerous. Isobilateral leaves with stomata present in equal numbers on both sides of the leaf show equal transpiration rates from both leaf surfaces. In the normal land plant approximately twenty per cent. of the transpiration consists of evaporation through the cuticle. In exceptional cases cuticular transpiration may be as low as one or two per cent. or be as much as fifty per cent. of the total, depending largely on the thickness of the cuticle.

In the leaf, water evaporates from the cell surfaces into the intercellular spaces with the result that the air in the sub-stomatal air-space becomes saturated with water-vapour, and provided the outside air is not saturated, water-vapour will diffuse out through the pore of the stoma. The rate of this outward diffusion depends on a variety of factors, but especially on the dimensions of the stomatal pores, and the external atmospheric conditions. The rate of evaporation of water from the leaf cells into the intercellular spaces of the leaf is governed to a great extent by the water-content of the cells. When these cells are turgid their walls are saturated with water and are probably covered with a film of " free " water which readily evaporates into the intercellular spaces. If the leaf is not fully turgid the cell-walls are still wet, but the film of water on the wall surfaces which abut on to the intercellular spaces is very thin and so offers a greater resistance to evaporation. Hence evaporation from these cell surfaces into the intercellular spaces is somewhat restricted. We speak of this condition as **incipient drying of the leaf,** and it is one of the most potent factors tending to restrict the amount of water transpired. Even under these conditions the air in the stomatal chamber will be more or less saturated and outward diffusion of water-vapour through the stomatal pore will tend to occur. The rate of this outward diffusion clearly will be influenced by the size of the pore.

Reference has already been made to the fact that the guard-cells of the stoma can, by altering their form, bring about changes in the dimensions of the stomatal pore. Their ability to do this depends mainly on the peculiar type of thickening of their walls. The guard-cells as seen in a transverse section have the form shown in Fig. 34, A. The wall remote from the pore is thin and the other walls are more or less thickened. When such a cell absorbs water from the adjacent tissues it becomes turgid and its volume increases. This increase in volume is made possible partly by a change in the shape of the cell and is brought about by the increased turgor. In this process the thin wall of the guard-cell bulges and the guard-cell appears to move slightly, so that the stomatal pore is opened. When the turgor of the guard-cells falls the movement is reversed and the stomatal pore is closed. In grasses the mechanism of the movement is rather different, but there again it is dependent on turgor changes in the guard-cells. Many factors affect the turgor of the guard-cells, and consequently the degree of opening of the stomata. Generally speaking, the stomata open in the light and close in the dark. Guard-cells, unlike other epidermal cells, contain chloroplasts, and on exposure to light they will therefore synthesise sugars. This brings about an increase in the osmotic pressure of the sap of these cells, which then absorb water from the adjacent cells. Their turgor thus increases and the stomatal pore opens. Light has a further effect on the guard-cells. In the dark these cells contain numerous starch grains. Exposure to light results in the conversion of this insoluble starch to soluble sugar, probably by enzyme action. As a consequence of this the guard-cells absorb water and become more turgid in the manner described above. When darkness supervenes the soluble sugar is reconverted to insoluble starch, turgor is lost and the stomatal pore closes. Drying of the leaf, whilst it often induces a temporary wide opening of the stomata, results finally in a loss of turgor by the guard-cells, with the result that the stomata close.

Slight changes in the degree of opening of the stomata have much less effect on the rate of transpiration than was formerly supposed. This is in part because the rate of loss of water through the stomatal pore is largely dependent on the water-content of the leaf as well as on the condition of the stomata (whether open or closed). Atmospheric conditions also are important. Water-vapour will diffuse out through the stomatal pore only when the air inside the leaf is nearer saturation point than the outside air. The drier the outside air the more rapid will be the outward diffusion and the greater will be the transpiration rate. Wind, by causing a rapid removal of water-vapour from the neighbourhood of the pore, and thus maintaining a relatively dry condition outside the stoma, will cause an increase in the rate of transpiration. Increase in temperature, too, brings about an increased rate of transpiration, partly because it accelerates the actual process of evaporation, whilst it also causes an increase in the apparent dryness of the outside air, the amount of water-vapour which can be present in the air before saturation point is reached being a function of temperature.

The observed rate of transpiration is dependent on the interaction of all these factors. Even when external conditions are identical different plants will transpire at different rates because of anatomical differences between them.

The **potometer**, a convenient form of which is represented in Fig. 125, may be used to demonstrate the effects of varying external conditions on transpiration. A bottle of about 300 c.c. capacity is fitted with a rubber stopper having three holes. Through one hole passes a measuring tube graduated in cubic centimetres, through another, the stem of a woody, leafy shoot, and through the third a funnel which acts as a water-reservoir. All joints should be air-tight. The bottle is filled with water and the stopper pressed home tightly. This causes the water to rise in the graduated tube, and the level is noted. After a short time it will be seen that the level of water in the graduated tube has fallen, and the amount of fall read off on the scale. The rate of fall gives a measure of the rate of water-absorption by the cut end of the shoot. If the apparatus is balanced on a pair of scales, left for a time, then weighed again, the loss in weight in grams represents the amount of water transpired. This loss is not necessarily identical with the amount of water absorbed by the shoot, although it is generally nearly so.

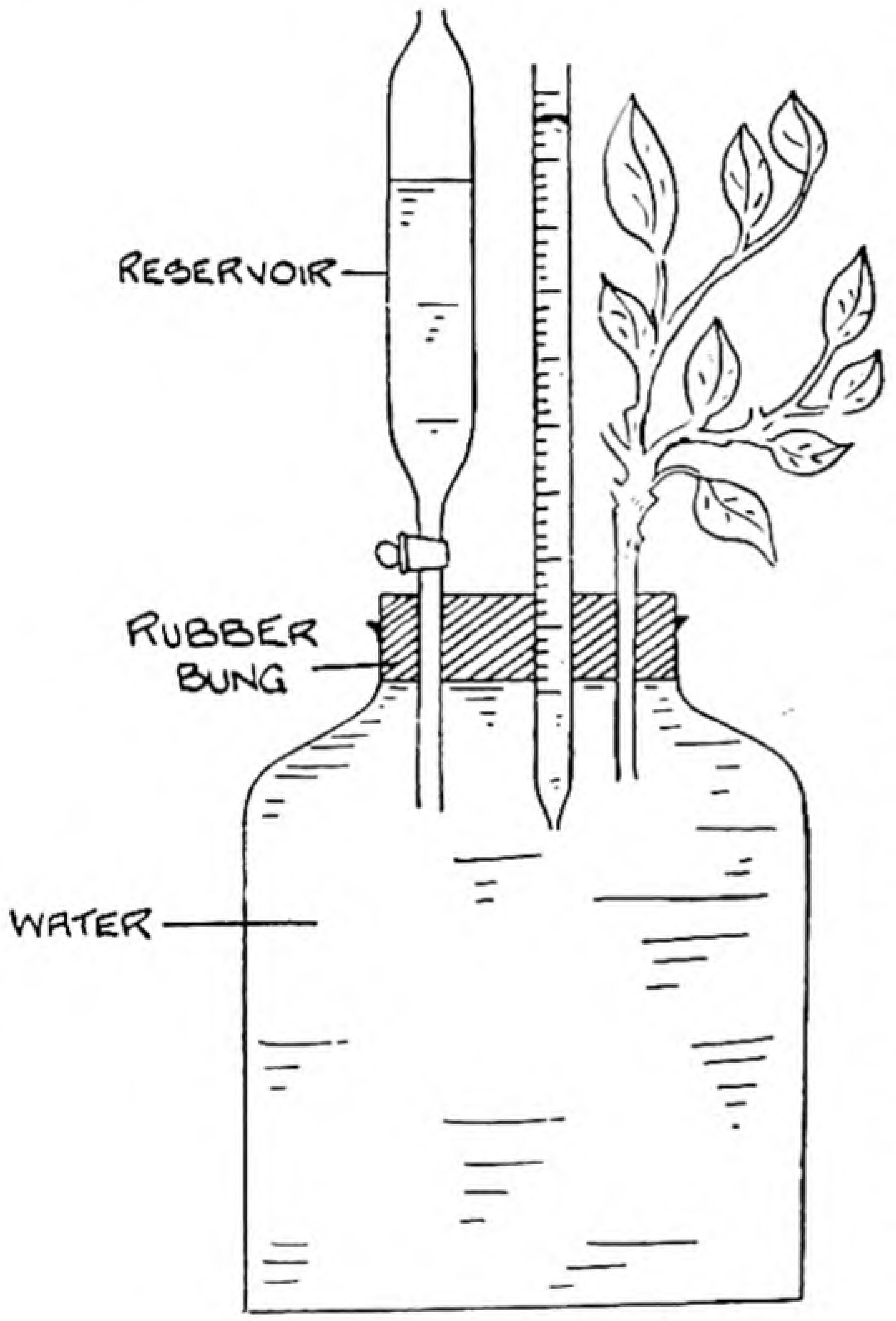


Fig. 125. POTOMETER.

The apparatus is conveniently portable, and so both absorption and transpiration rates of the shoot can be determined under varied conditions.

12. The Ascent of Water in the Plant

We have already dealt with the process of water absorption by the roots and have considered the salient features of transpiration. Before the absorbed water can be transpired it has to be conducted to the transpiring surface, and this usually involves the raising of the water against the downward pull of gravity. We have seen that this upward transport of water takes place in the xylem and it has been pointed out that in the roots a pressure, forcing water some distance up the stem and known as root pressure, may develop. Sometimes the exudation of sap under the influence of root pressure from the stump of a plant after decapitation is very marked, especially in the spring. Thus, if the stem of a vigorous young vine is cut in spring about a foot from the ground, there is an abundant exudation of watery sap from the vessels at the cut surface. This phenomenon is called "*bleeding*," and its manifestation continues for a considerable time.

Root pressure can readily be demonstrated with a potted plant

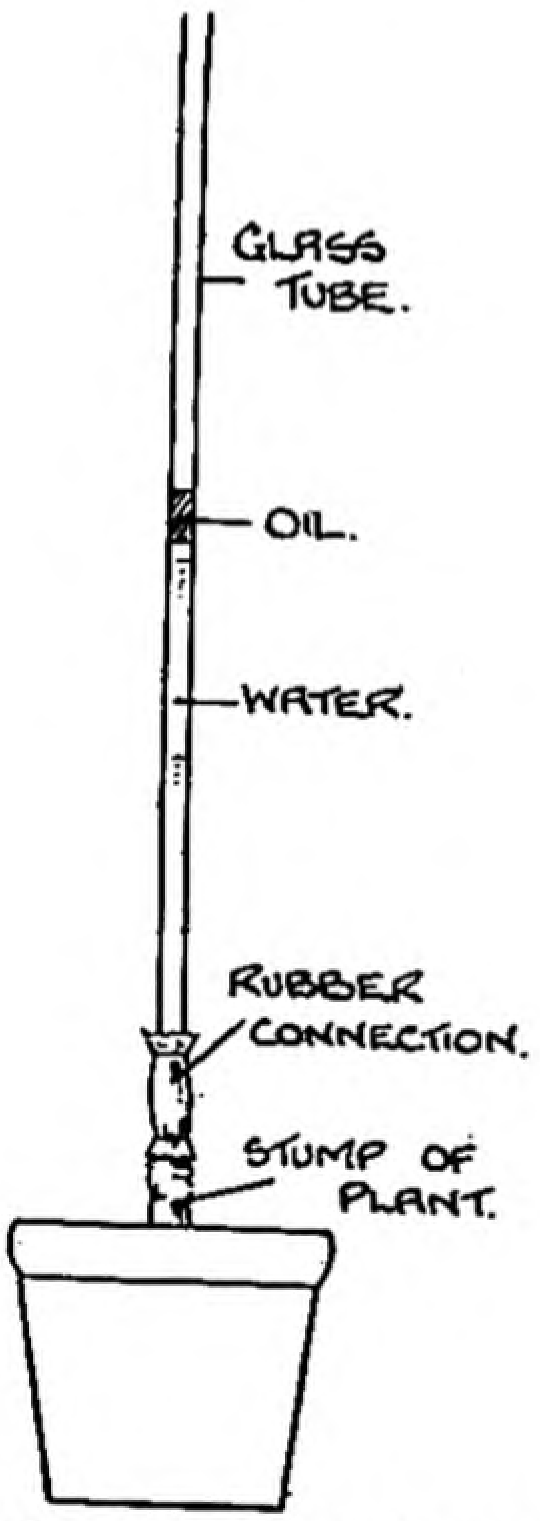


Fig. 126. Root Pressure.

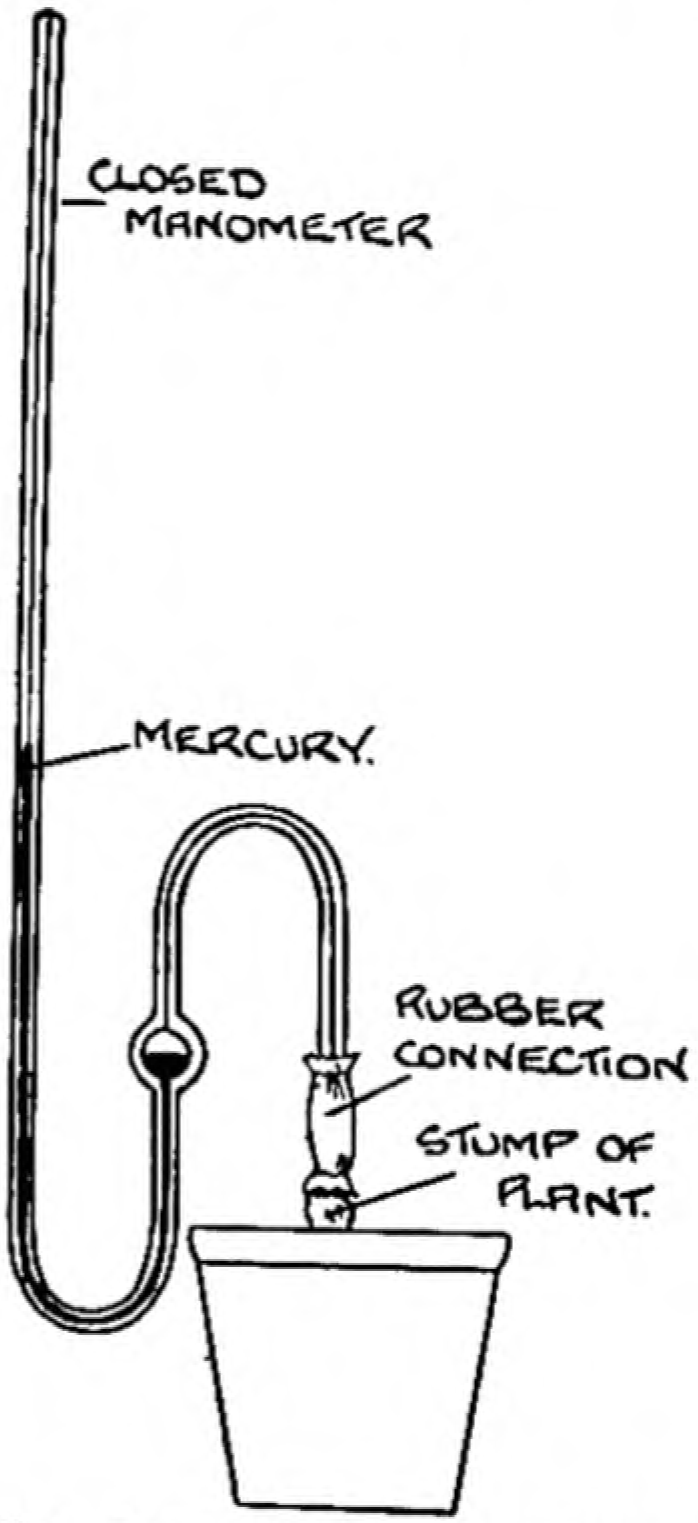


Fig. 127. Root Pressure, Manometer Attached.

(Fig. 126). An actively growing fuchsia or similar plant should be used and the shoot cut off a few centimetres from the soil-level. If the stump is connected by means of rubber tubing to a vertical glass tube the liquid which has been exuded from the stump will soon appear in the glass tube, and if the diameter of the tube is known the volume of sap exuded can be calculated. When this is done it is found that the amount of liquid exuded from the stump is rarely sufficient to cover the transpiration requirements of the intact plant. If instead of attaching a vertical glass tube to the stump a mercury manometer (Fig. 127) is used, it is possible to measure the root pressure and to express it in atmospheres.

Bearing in mind that a root pressure of one atmosphere is sufficient to raise water to a height of approximately thirty feet, we find that observed root pressures, which may vary from *nil* to one atmosphere, but rarely more, might account for the upward movement of water to the leaves of some herbaceous plants, but are never of sufficient magnitude to raise water to the leaves of large trees. Further, root pressure generally shows a seasonal fluctuation, being at a maximum in the spring and at a minimum in the summer when the water requirement of the leaves is greatest. Clearly, root pressure alone cannot account for the ascent of water in vascular plants. In the leaves, owing to transpiration, many of the mesophyll cells will not be fully turgid. The whole of the osmotic pressure of the vacuolar solution of these cells will not be used up as turgor pressure, and the cells will exhibit a suction force and absorb water from the tracheides and vessels of the veins of the leaf. The conducting elements of the xylem of the plant form a continuous system, and if some water is abstracted from this system by the living cells of the leaf, the remaining contents of the xylem will be in a state of tension. A column of liquid water exhibits considerable cohesive properties, and when subjected to a tension the column will stretch somewhat and will not break. The column behaves in some respects as a solid, and a pull exerted at one point in the column is transmitted to all its parts. The xylem of the plant is surrounded by living cells and we can consider, therefore, that when a pull is exerted by the living cells of the leaf at the top of the system, the pull is transmitted, and the whole column of water tends to move upward. The osmotic pressure of the sap of leaf-cells represents the maximum pull which can be developed, and this may be as much as twenty atmospheres. The tensile strength of water is such that a pull of this magnitude can be transmitted by it, and so we have here a mechanism capable of lifting water to a height

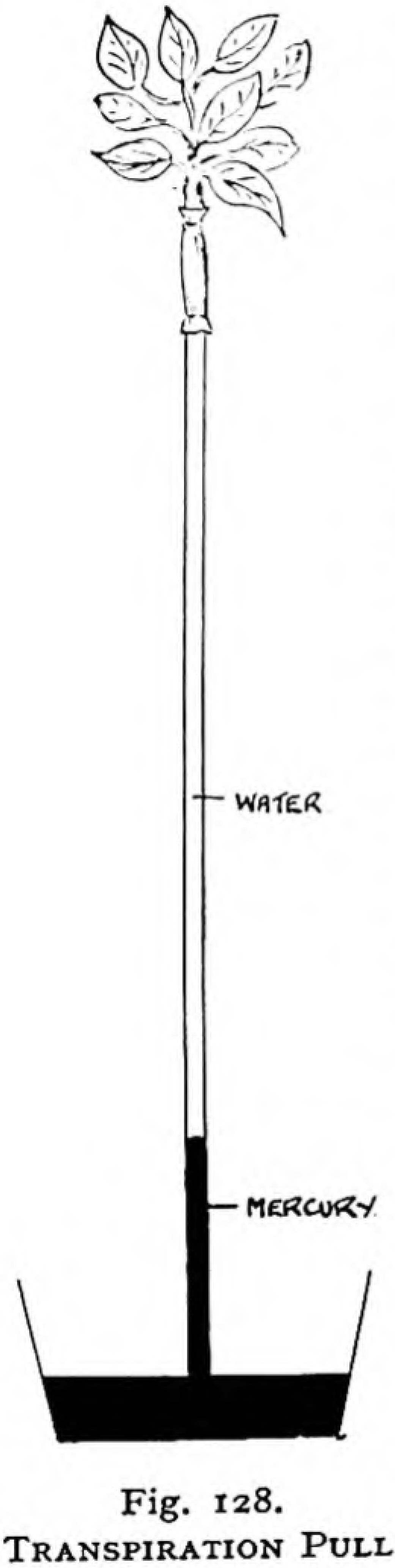


Fig. 128.
TRANSPIRATION PULL.

of six hundred feet. Further, as the contents of the xylem are in a state of tension they will be exerting a pull on the water of the surrounding tissues, and this pull will facilitate the passage of water from the living pericycle cells of the root into the vessels of the xylem. We conclude, therefore, that the living cells of the leaf may exert a pull, known sometimes as **leaf suction**, and that this pull, because of the cohesive properties of water, is able to effect an upward movement of water in the xylem so that the supply of water to the leaves of even the highest trees is maintained. Further, as poisonous solutions will ascend the stem, it is concluded that the living cells of the stem do not play any important part in the process.

The force of leaf suction may be utilised to raise liquids in a glass tube. A rhododendron or other woody shoot is fixed to a narrow glass tube which is filled with recently boiled and cooled distilled water, and set up as in Fig. 128 with its lower end dipping into mercury. The shoot transpires and replaces the water thus lost by absorbing water from the glass tube. Because of the cohesive properties of liquids the column of water in the tube rises and the mercury rises after it. Frequently the rise of mercury exceeds 76 cm., *i.e.* it exceeds the level to which it could be raised by atmospheric pressure alone.

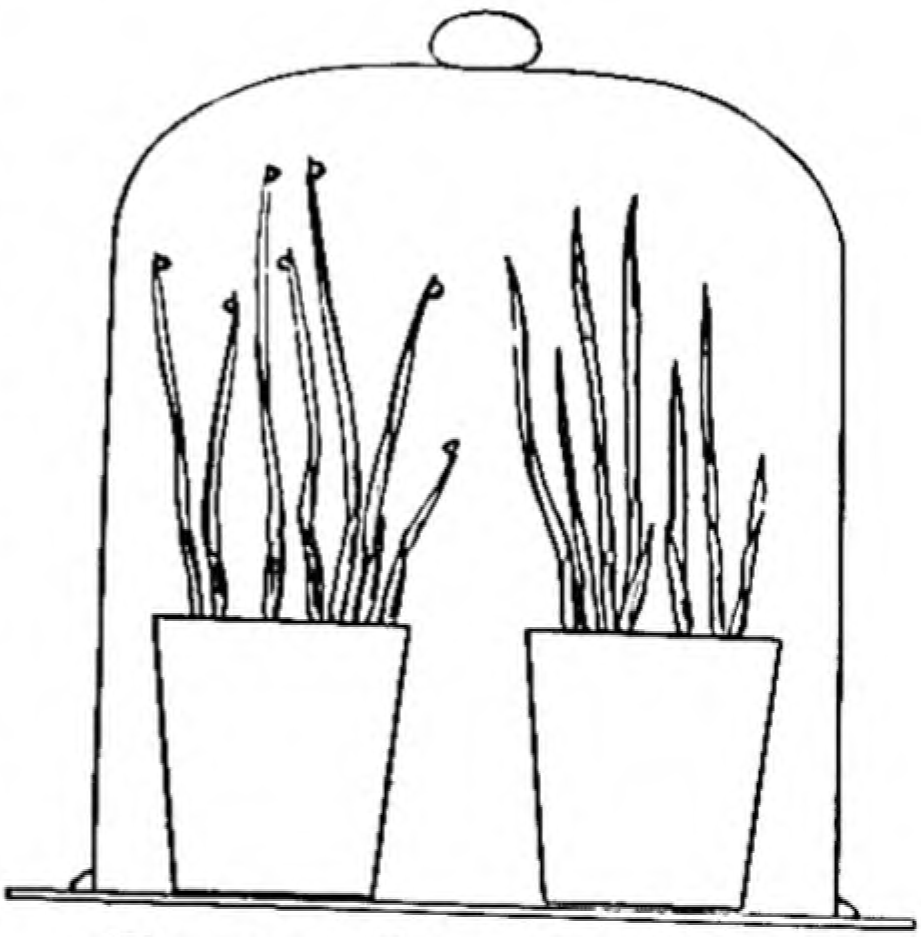


Fig. 129. GUTTATION, *Avena* SEEDLINGS.

13. Guttation of Liquid Water

Under suitable conditions liquid water may be forced out of leaves. This usually happens when water absorption is occurring freely and considerable root pressure is developed, whilst atmospheric conditions are such that transpiration proceeds at only a very low level, if at all. The seedlings of many cereals frequently *guttate* liquid water in this way. If, for instance, a pot of oat seedlings is well watered and placed in a saturated atmosphere drops of water are soon seen at the apices of the leaves (Fig. 129, left). This guttation of liquid water is shown not only by cereals but by the garden nasturtium (*Tropaeolum*), certain saxifrages, and many other plants. The water escapes through special water stomata (Fig. 37). In the case of some saxifrages the secreted water contains calcium salts in solution, and when the water evaporates the salts are left and form a white incrustation on the toothed margin of the leaf. The dependence of guttation on active water absorption by the root is shown if a pot of oat seedlings is well watered with a ten per cent. salt solution. The roots are then surrounded by a solution having an osmotic pressure greater than that of the sap of the root-hairs and so the osmotic entry of water into the root-hair is not possible. Under these conditions no guttation of liquid water from the leaves takes place although they are surrounded by a saturated atmosphere (Fig. 129, right).

The drops of "dew" which are a familiar sight on grass leaves early in the morning, after a warm humid night, consist mainly of water which has guttated from the leaves. At night conditions are especially favourable for guttation. The air is frequently saturated and so transpiration does not take place. Water absorption by the roots, however, continues, root pressure develops, and under its influence guttation takes place.

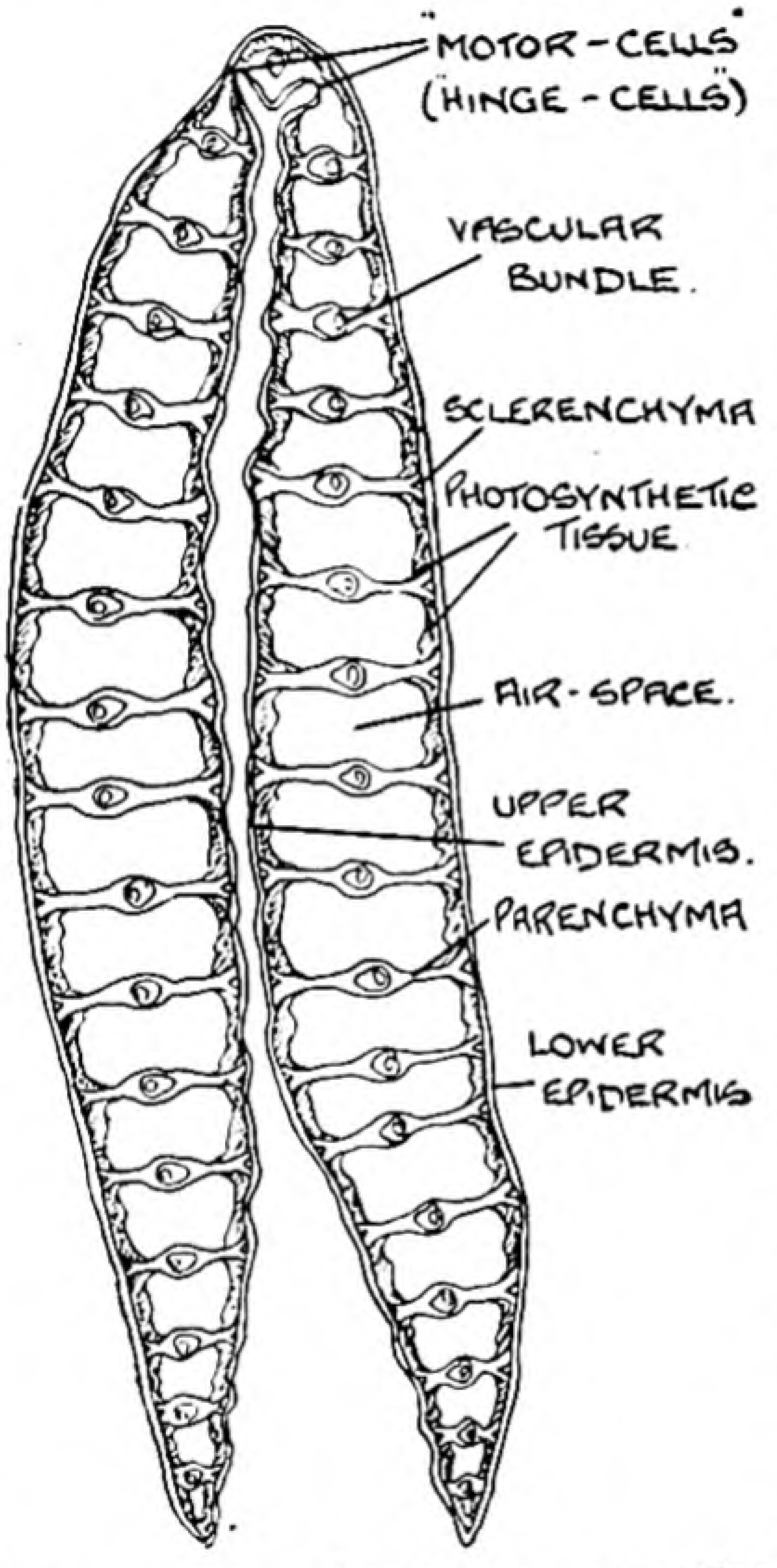


Fig. 130. *Catabrosa aquatica.* TRANSVERSE SECTION OF LEAF (DIAGRAMMATIC) TO SHOW SYSTEM OF AIR-SPACES.

14. Importance of Transpiration

It has been claimed that transpiration promotes absorption of salts, and their conduction, and that it exerts a cooling effect on the transpiring organs. There can be little doubt that the existence of an upward moving current of water—the transpiration stream—in the xylem, facilitates the upward conduction of salts in the plant. Water-absorption and salt-absorption by the roots, however, constitute two distinct phenomena, and it is unlikely that the latter is much influenced by the former. A cooling effect of transpiration is to be expected in so far as a proportion of the energy of the heat rays falling on the leaf is used in the vaporisation of water. The exact importance of this cooling effect is difficult to assess. In spite of its possible harmfulness to the plant when excessive, transpiration is not to be regarded as a necessary evil. By its means the upward transport of solutes in the xylem is facilitated whence supplies reach the leaf cells.

Evaporation of the water from the transpiring surfaces will help to prevent excessive heating and at the same time leave the salts in the cells for use by the plant.

15. Mesophytes

Water intake, water transport and water loss have been considered chiefly in so far as they occur in what we think of as a normal land plant. Such plants, with thin leaf-blades, showing no special protection against excessive transpiration, are termed **mesophytes.** Mesophytes are found growing mainly in situations where the soil is not habitually water-logged and where extreme drought conditions are not experienced.

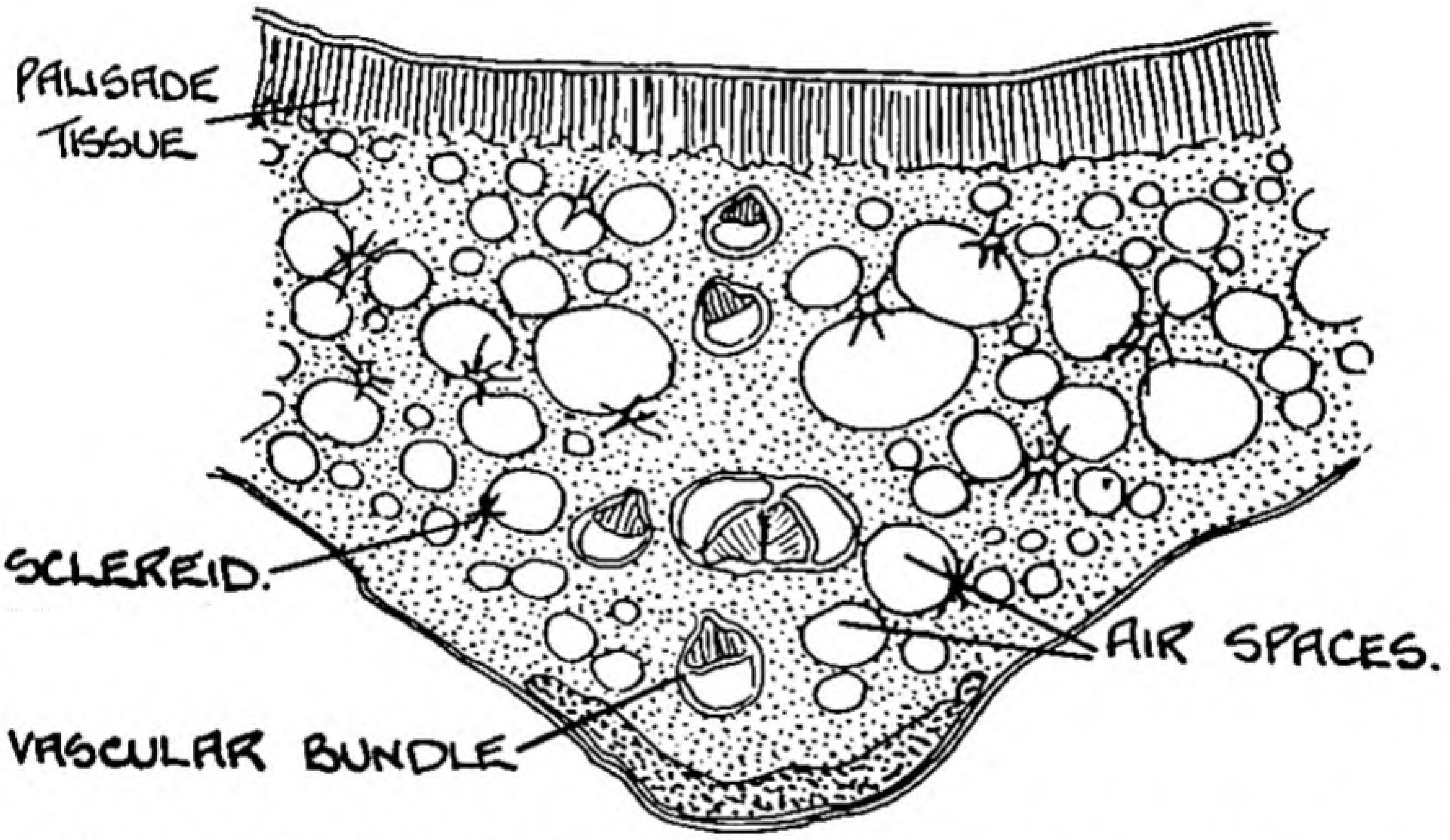


Fig. 131. T.S. PETIOLE OF WATER LILY (DIAGRAMMATIC) TO SHOW AERATING SYSTEM.

16. Hydrophytes

Hydrophytes are plants which live where there is an abundant supply of water. If they are completely submerged they cannot, of course, transpire. Other hydrophytes which may be rooted in the mud at the bottom of a pond or river may have floating leaves or even aerial shoots, and these exhibit normal transpiration. The air surrounding the transpiring surfaces is generally moist and hence transpiration is restricted. Correlated with the permanently low transpiration rate and the ease of water absorption there is generally a very poorly-developed conducting system. One characteristic of many hydrophytes is the presence of large air-spaces in the tissues, especially those of the underwater organs. Consequently the internal passage of air is facilitated and a supply of oxygen to the living cells of the submerged organs assured.

17. Xerophytes

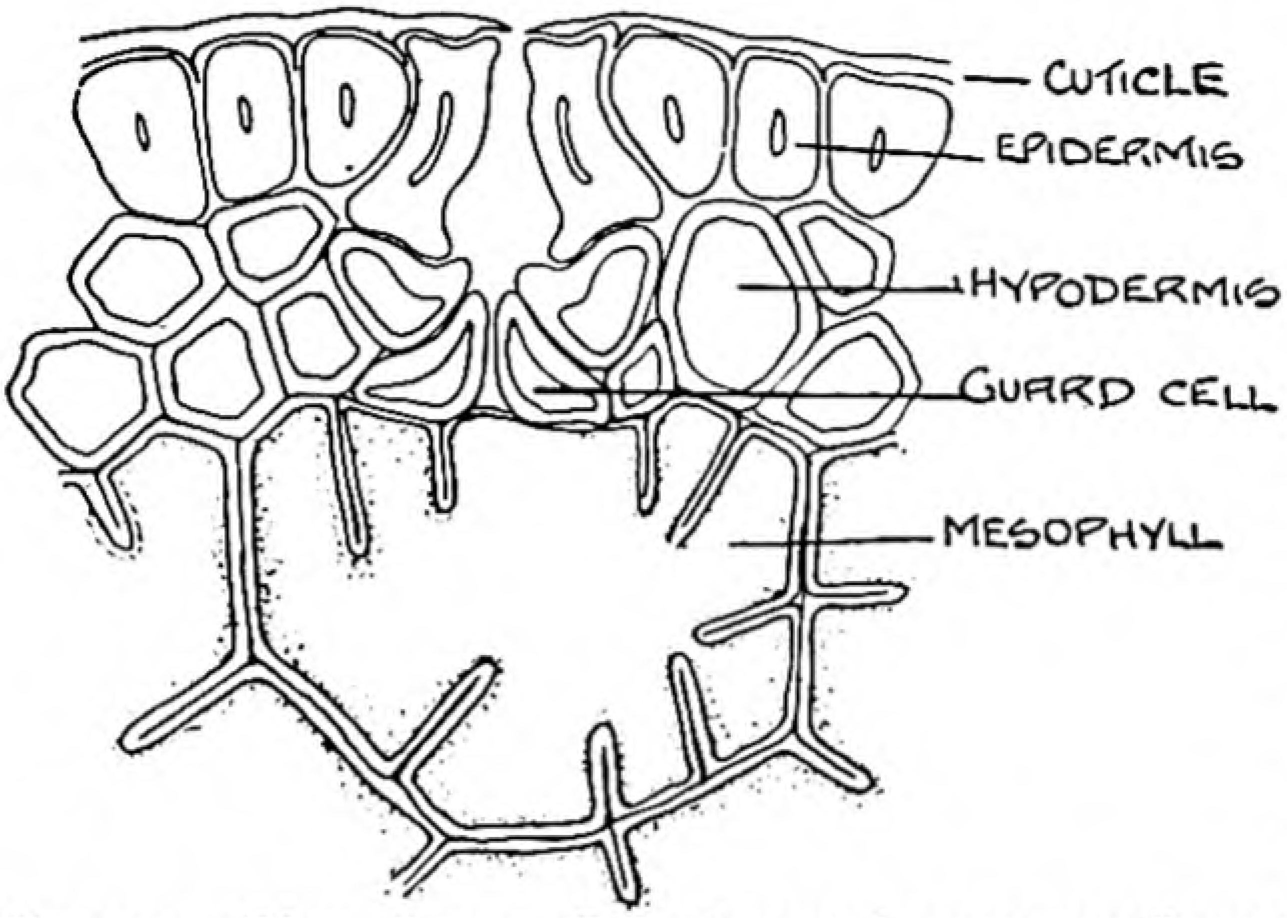


Fig. 132. *Pinus* LEAF. T.S. OUTER LAYERS OF CELLS.

The term **xerophyte** was first applied to plants of dry places where the water supply is scanty and irregular, and where atmospheric conditions are such as to favour a high rate of transpiration. Plants in these situations have an obvious need to economise so far as their water supply is concerned. A lavish expenditure of water in transpiration is clearly undesirable if the plants are to avoid excessive desiccation. The plants of these arid regions frequently exhibit peculiarities of form, many of which can be interpreted as checks to transpiration. In some the stomata are sunk in pits instead of being flush with the surface as they are in many mesophytes. Sunken stomata of this nature occur in *Pinus* (Fig. 132), *Hakea* (Fig. 133), etc., whilst in the Oleander (*Nerium Oleander*) the stomata are in groups and in irregular depressions in the leaf surface (Fig. 134). The depressions undoubtedly protect the stomata against the drying effect of wind, and to that extent reduce the transpiration rate. Permanent protection of the stomata does not always occur. Many xerophytic grasses have the stomata confined to one surface, and when there is a deficiency of water the leaves roll up so that

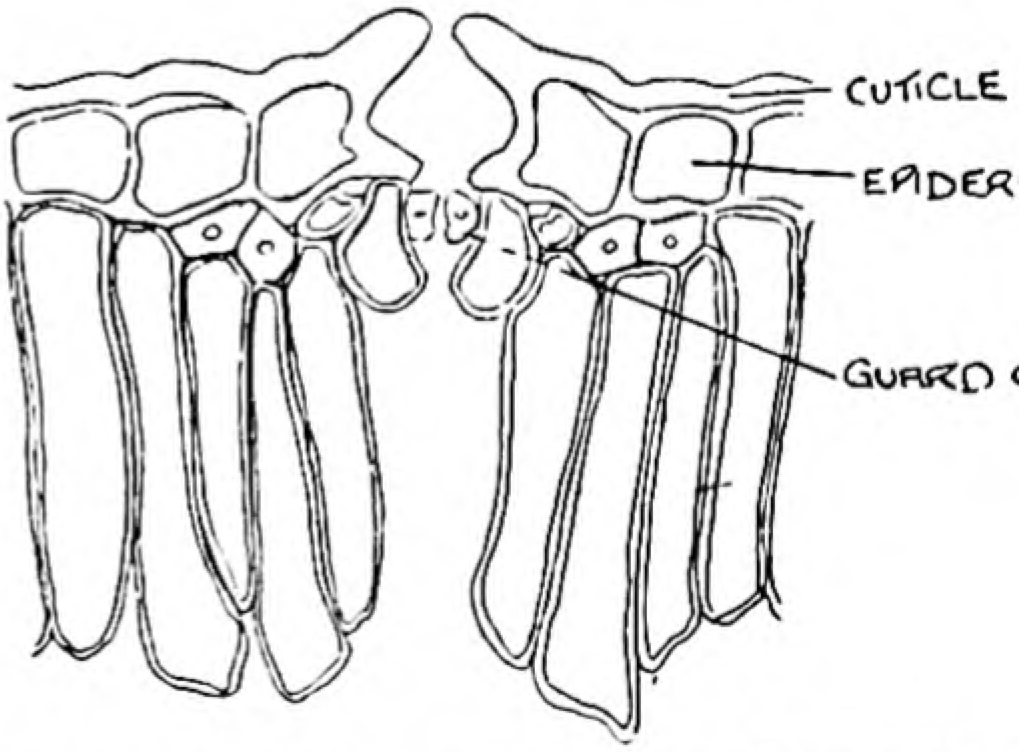


Fig. 133. *Hakea* LEAF. T.S. OUTER LAYERS OF CELLS.

all the stomata are on the inner surface of the rolled leaf. The air enclosed by the rolled leaf quickly becomes saturated with water and outward diffusion of water-vapour through the stomatal pores ceases.

Rolling of the leaf with a consequent protection of the stomata is well seen in the sand-dune grass, *Ammophila arenaria* (Fig. 135). Here, when the leaf is flat, the upper surface is seen to consist of a series of parallel ridges and grooves, and at the base of each groove the epidermal cells are large and thin-walled. In other parts of the leaf the epidermal cells have thick walls, and the exposed walls are strongly cuticularised. The stomata are found on the sides of the ridges and are absent from the lower surface of the leaf. When transpiration is active the leaf loses water. The thin-walled epidermal cells at the bases of the grooves—the hinge- or motor-cells—lose water more quickly than the rest and contract, and tend to draw the two sides of the groove together. Thus the leaf rolls into a cylinder with the lower epidermis on the outside.

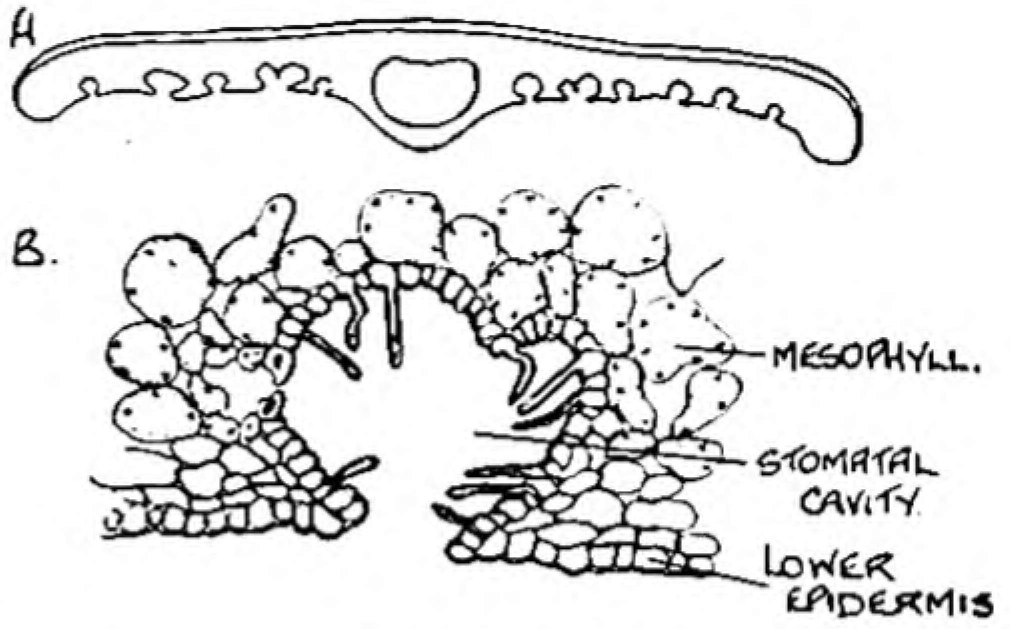

A
B.
MESOPHYLL.
STOMATAL CAVITY
LOWER EPIDERMIS

Fig. 134. OLEANDER LEAF. T.S.
A, Diagrammatic; B, Lower surface, magnified.

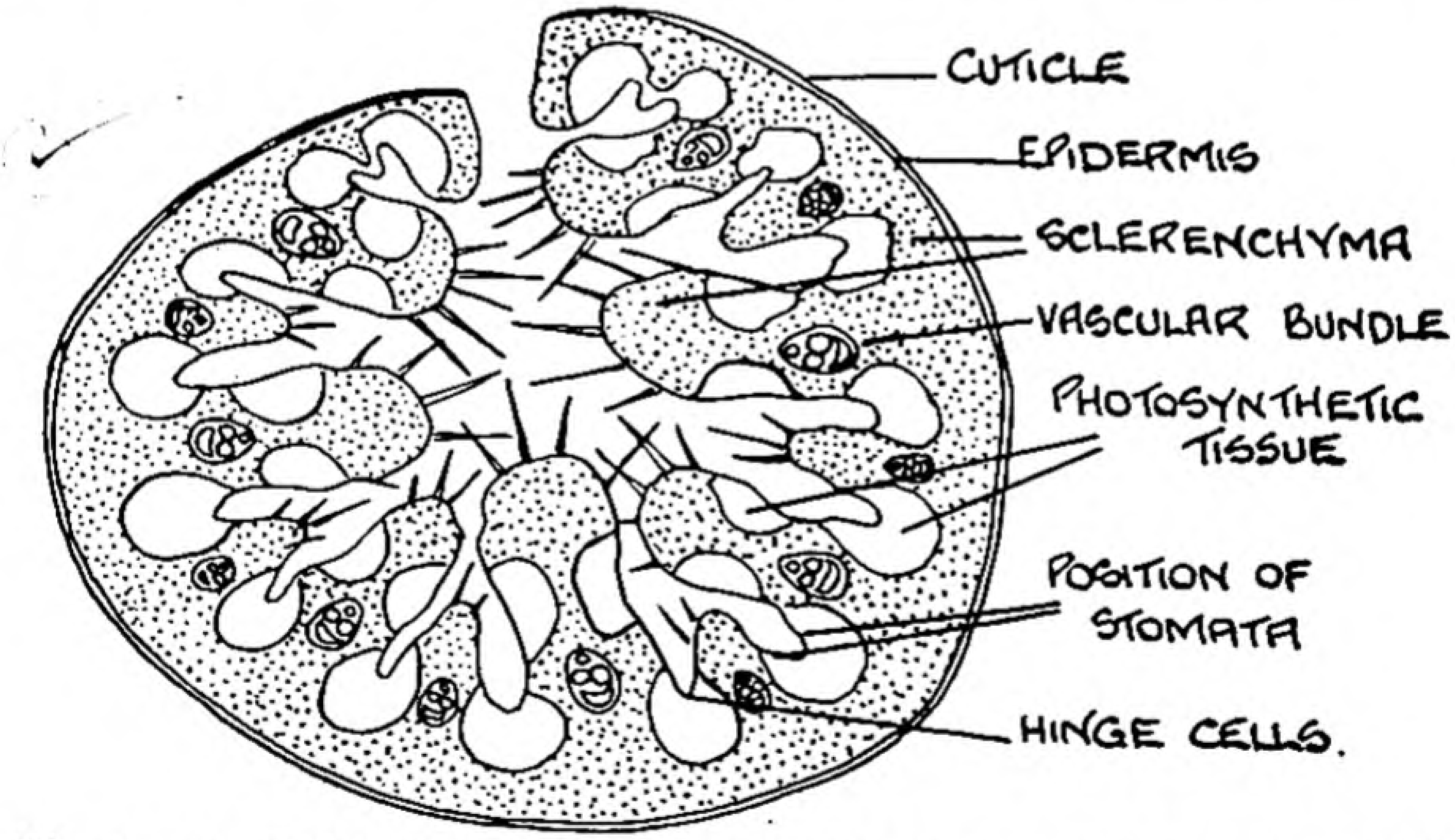

CUTICLE
EPIDERMIS
SCLERENCHYMA
VASCULAR BUNDLE
PHOTOSYNTHETIC TISSUE
POSITION OF STOMATA
HINGE CELLS.

Fig. 135, A. TRANSVERSE SECTION (DIAGRAMMATIC) OF LEAF OF *Ammophila arenaria*, SHOWING PROTECTED STOMATA.

Protection against wind and excessive insolation may be afforded by a covering of hairs. A reduction in the transpiring surface is sometimes effected by the possession of small leaves (as in many species of *Erica*), by the development of leaf spines (e.g. *Ulex*, gorse, Fig. 112, C) instead of broad, flat leaves, or by the shedding of leaves in the dry season (e.g. *Cytisus*, broom), leaving the functions normally carried out by the leaf to be conducted by the green stems. This latter condition is shown well in *Casuarina* (the Australian she-oak, Fig. 137). The leaves are small, brown and scale-like, and the normal leaf functions are carried out by the stem. The stomata are protected by being sunk in deep longitudinal grooves. Xerophytes, too, are on the whole, characterised by the possession of a thick cuticle which restricts cuticular transpiration. Wax may also form a protective layer on the epidermis. Many plants without protected stomata possess remarkable drought-resisting powers. When they are well supplied with water they transpire at a rate which may exceed that exhibited by mesophytes. When the water supply becomes deficient they at first continue to transpire rapidly, then the stomata close, and since the plants possess a thick cuticle, transpiration is reduced to a very low level, as cuticular transpiration is only slight. In mesophytes, on the other hand, cuticular transpiration goes on, and so water is lost at an appreciable rate from the leaves even when the stomata are closed. The xerophytes, then, are characterised not by a low transpiration

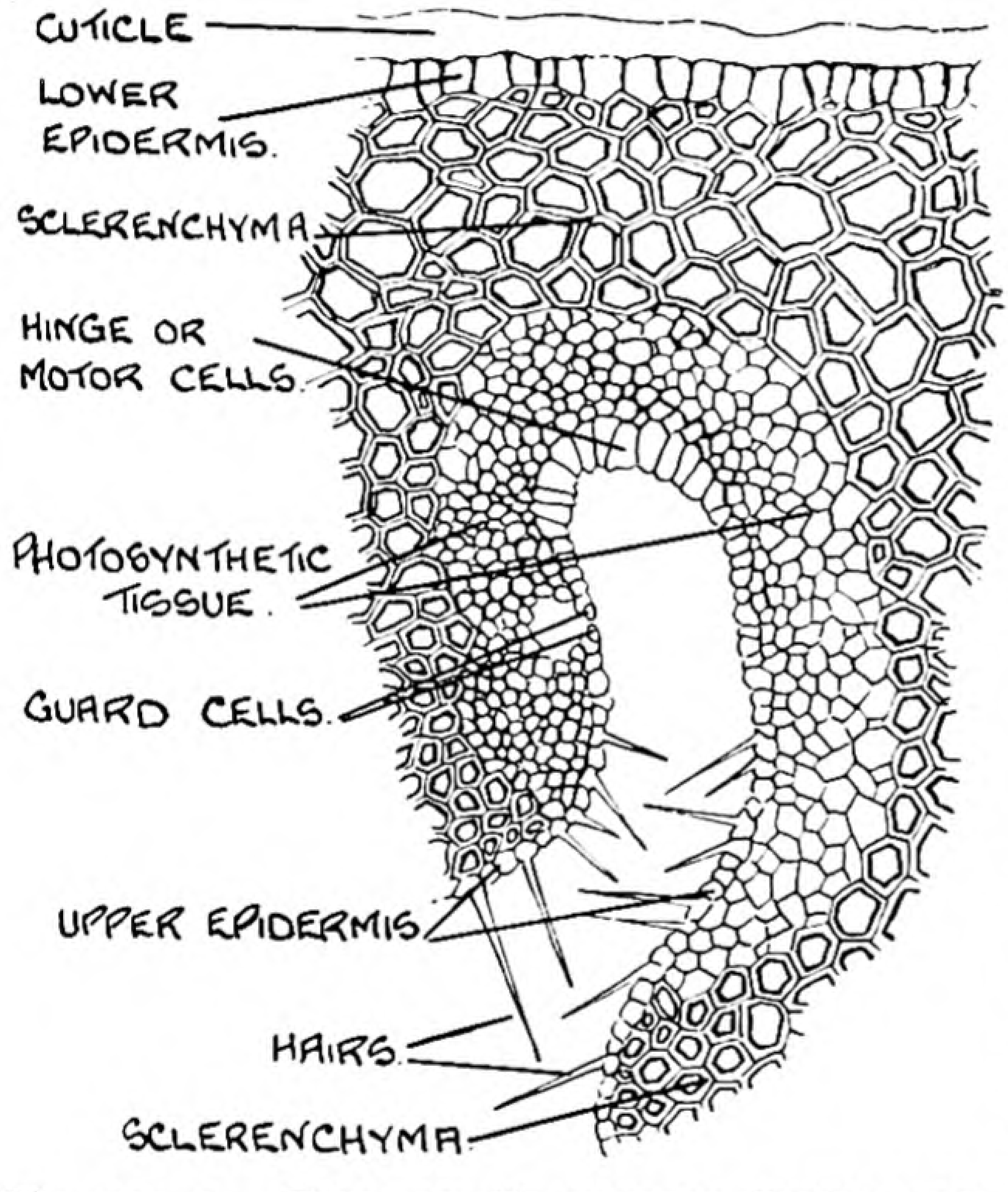


Fig. 135, B. PART OF TRANSVERSE SECTION OF LEAF OF *Ammophila arenaria*, BETWEEN TWO RIDGES, IN DETAIL.

rate, but by the ability to reduce the transpiration rate considerably when the water supply is deficient. Many xerophytes, too, can endure, unharmed, a degree of desiccation which would be fatal to mesophytes. Their cells can remain in a non-turgid condition for long periods, and then regain their turgidity when the water supply is renewed. Under similar conditions the cells of the mesophyte would die.

A further method of mitigating the effect of water shortage is by the development of water-storage tissue. Many desert plants possess succulent stems (*Kleinia articulata*, *Euphorbia larica*, *Opuntia*

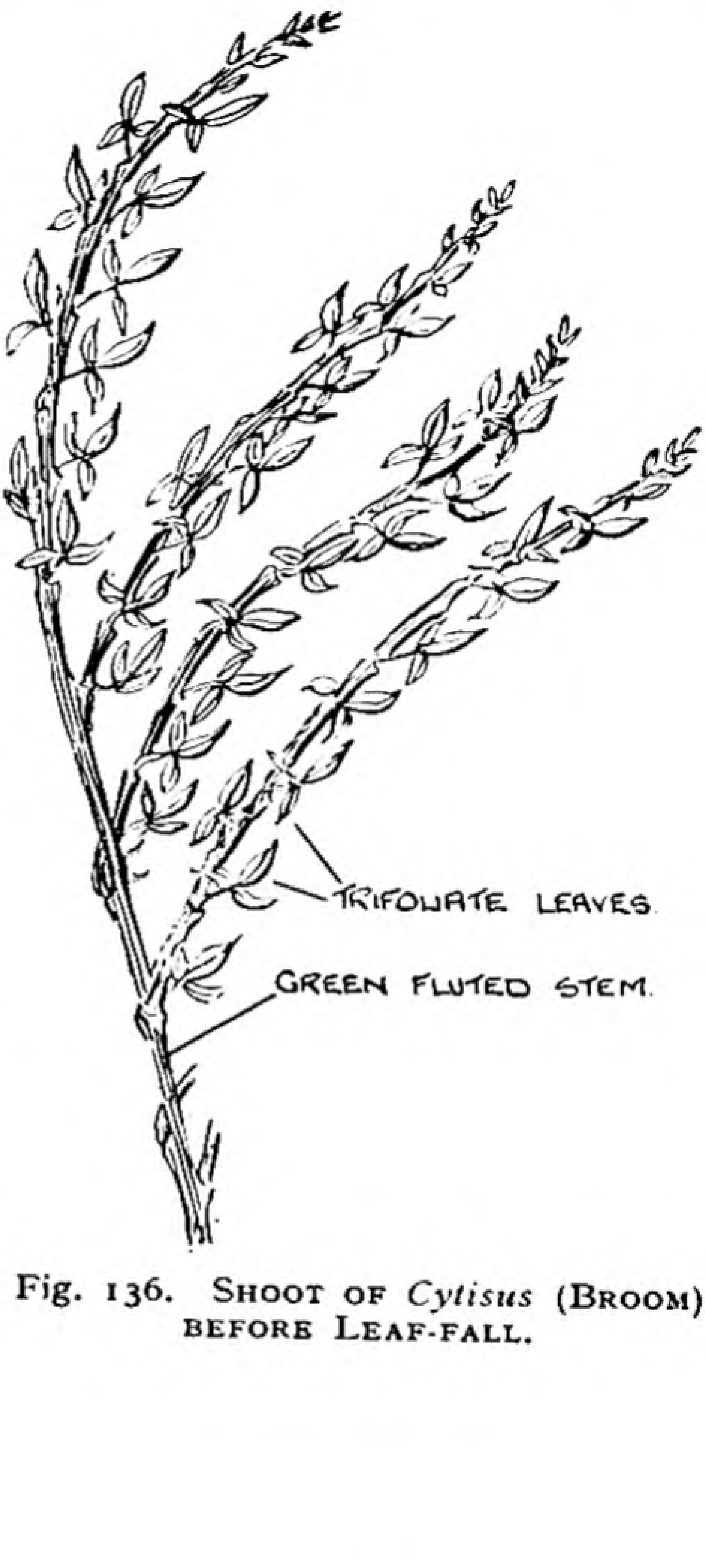

TRIFOLIATE LEAVES
GREEN FLUTED STEM.

Fig. 136. SHOOT OF *Cytisus* (BROOM) BEFORE LEAF-FALL.

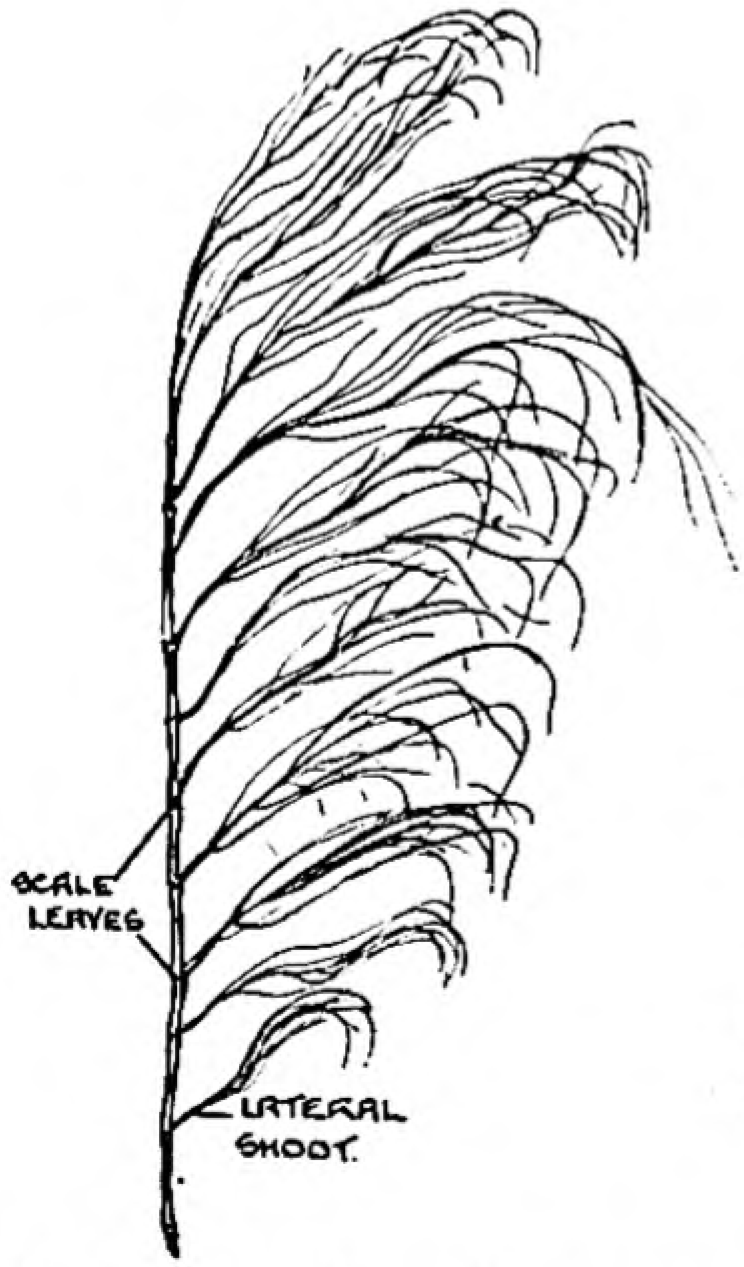

SCALE LEAVES
LATERAL SHOOT.

Fig. 137, A. *Casuarina*, EXTERNAL.

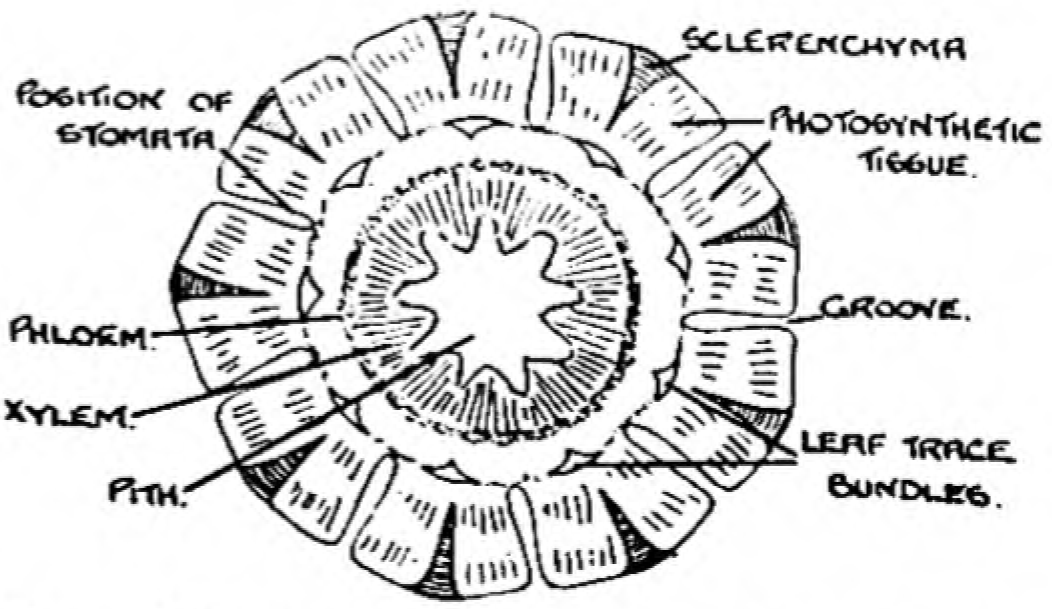

SCLERENCHYMA
POSITION OF STOMATA
PHOTOSYNTHETIC TISSUE.
GROOVE.
PHLOEM
XYLEM
PITH
LEAF TRACE BUNDLES.

Fig. 137, B. *Casuarina*, T.S. STEM.

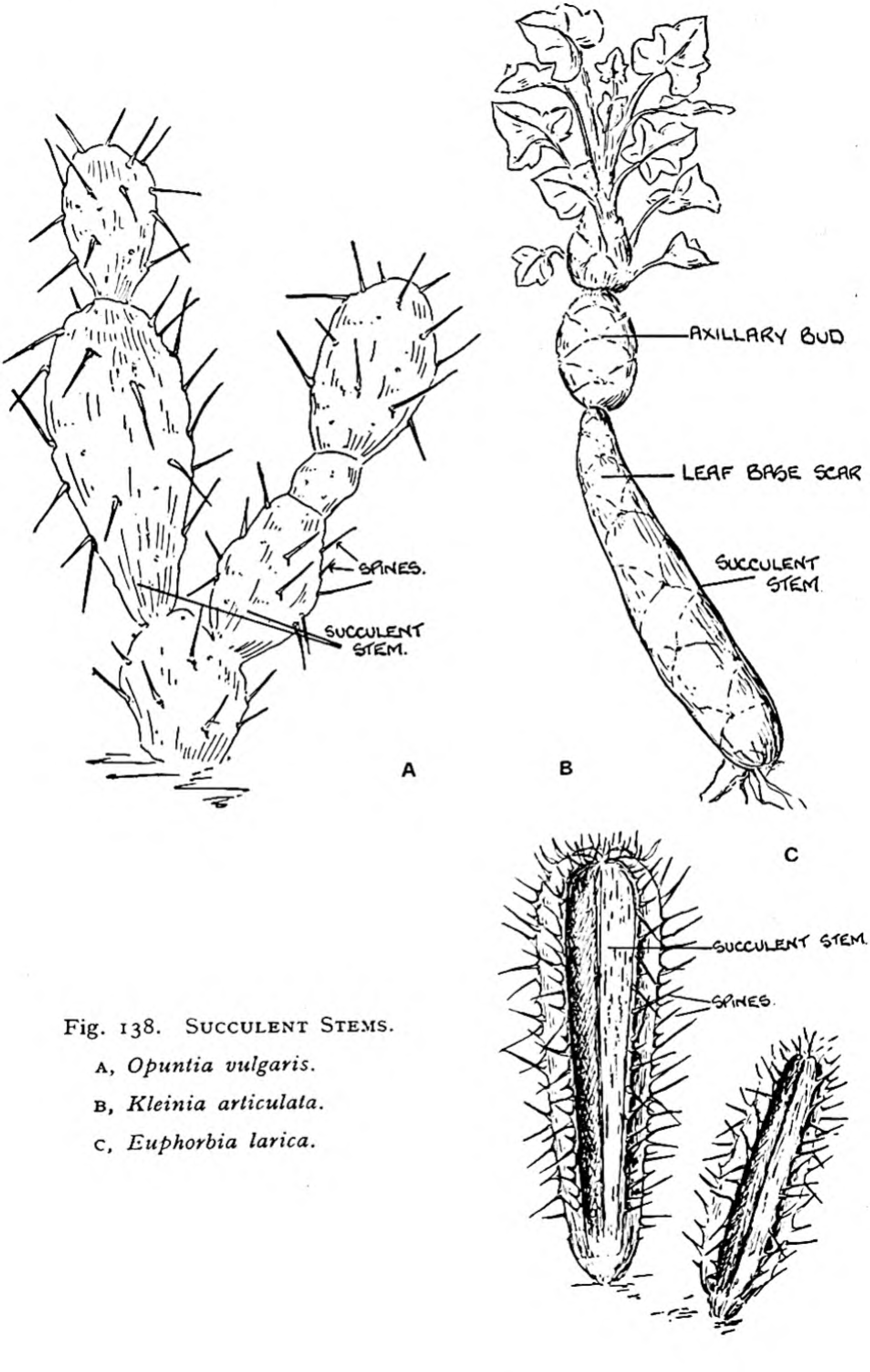

SPINES.
SUCCULENT STEM.
A
AXILLARY BUD
LEAF BASE SCAR
SUCCULENT STEM
B
C
SUCCULENT STEM
SPINES

Fig. 138. SUCCULENT STEMS.

A, *Opuntia vulgaris.*

B, *Kleinia articulata.*

C, *Euphorbia larica.*

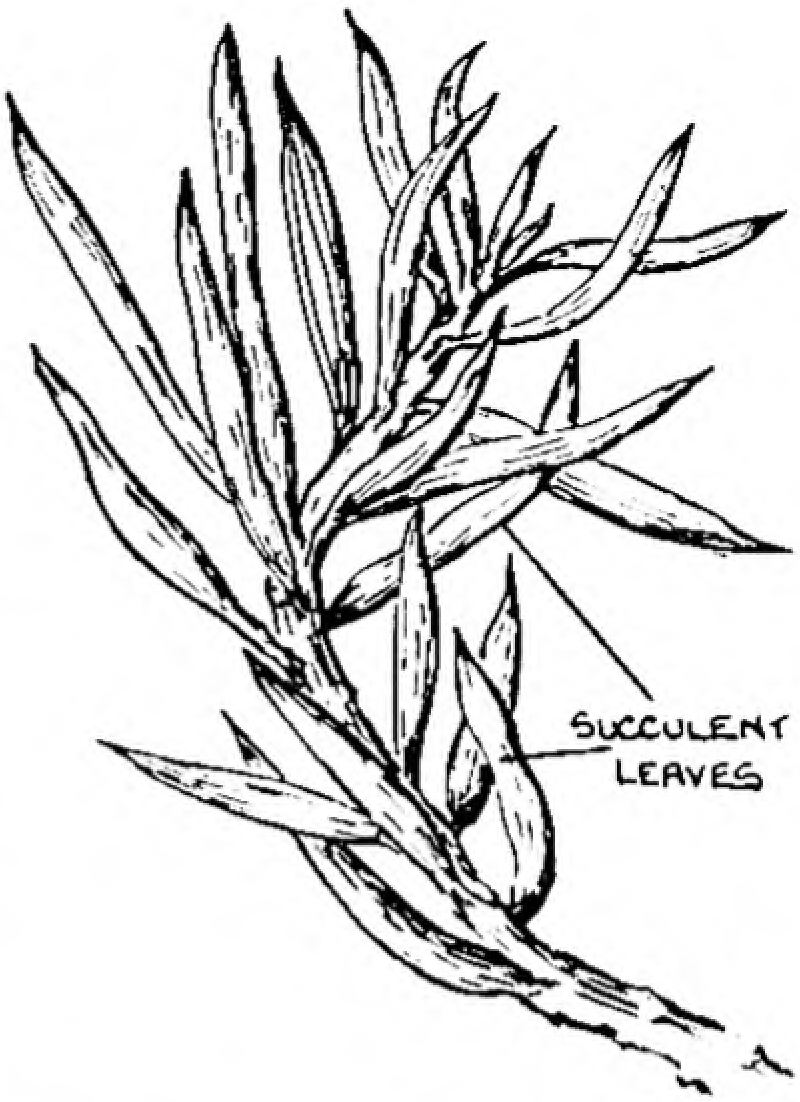


Fig. 139, A. *Kleinia ficoides.*

vulgaris, Fig. 138) or leaves (*Kleinia ficoides*, *Mesembryanthemum*, Fig. 139, *Aloe*, Fig. 140), which consist largely of special parenchymatous tissue used for the storage of water. These plants, too, often have an extensive root-system so that they exploit a large volume of soil. When rain falls water is quickly absorbed and stored and then expended slowly during periods of drought. The slow expenditure of water is due to the possession of few stomata, which may be protected, a thick cuticle, and probably also the mucilaginous character of the cell contents. A more obvious way of escaping the effect of drought is by the cessation of vegetative activities. Many bulbous plants pass through the dry season in a condition of rest. Deciduous trees of the North Temperate Zone (oak, ash, beech) shed their leaves in the autumn and so do not transpire during the winter, when, owing to low soil temperature, water absorption by the roots is slow.

Many of the special structural features exhibited by plants of dry places and interpreted as constituting checks to transpiration are also found in plants growing where the water supply appears to be abundant. These plants, too, have been considered as xerophytes because they look like them. It is better to refer to them as xeromorphic plants, that is, plants showing the modifications of form which we associate with plants of dry places. In this category would fall the halophytes, *i.e.* plants of salt marshes (e.g.

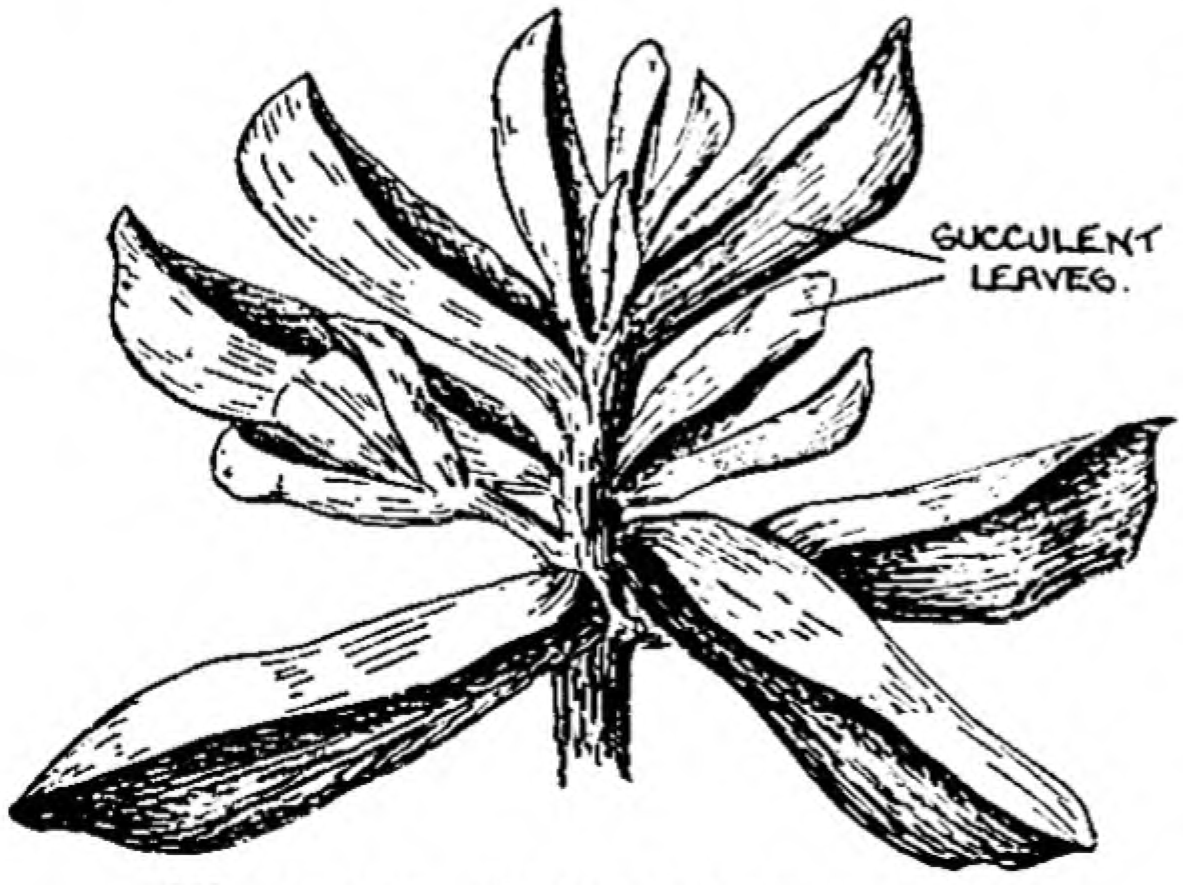


Fig. 139, B. *Mesembryanthemum sp.*

Salicornia, Suaeda, Obione, etc.) which are flooded periodically with salt water, and the plants of wet moors (*Molinia, Empetrum,* etc.). It has been suggested that in these situations a state of "physiological drought" exists, and that, although an abundance of water is present, water-absorption by the roots is difficult so that the plants do suffer from water shortage. Conclusive evidence on this point is lacking.

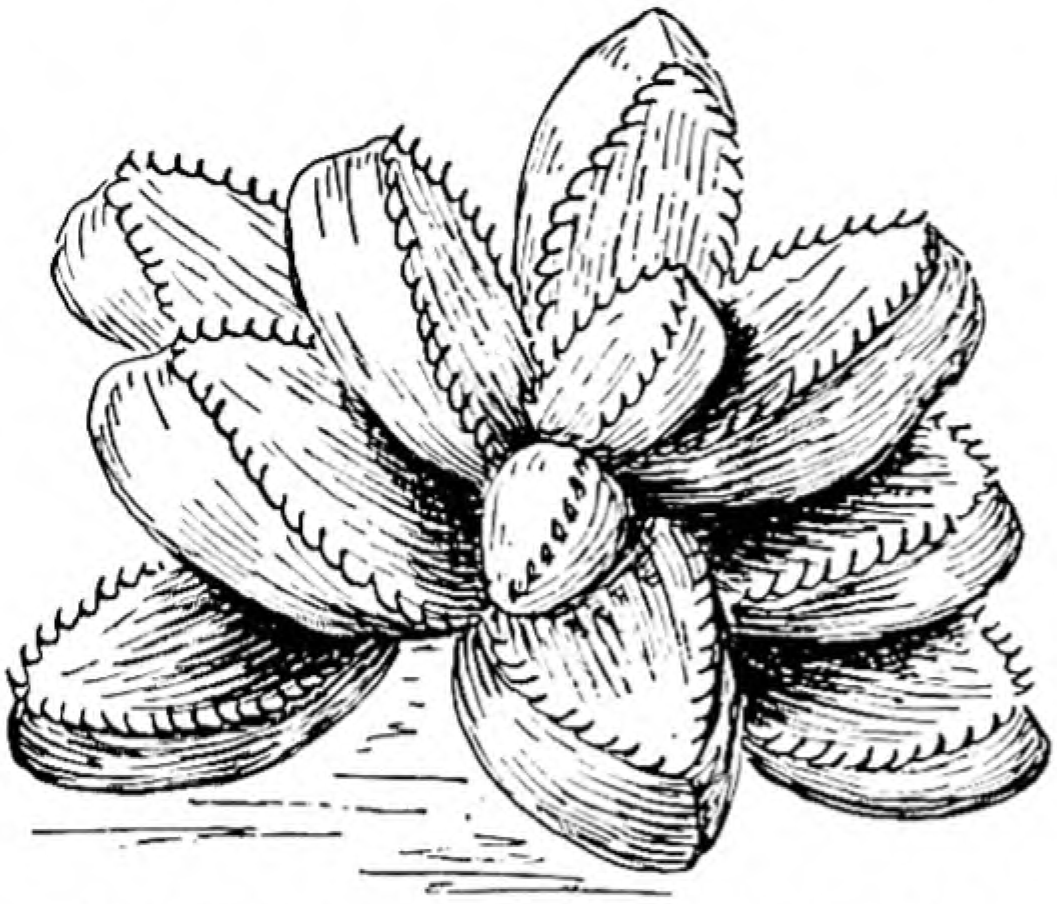


Fig. 139, c. *Mesembryanthemum, sp.*

18. Photosynthesis (Carbon Assimilation)

We have already pointed out (pp. 9 and 19) that the carbon, which constitutes about forty per cent. of the dry weight of the plant, is derived from the air. The carbon dioxide of the atmosphere is absorbed, especially by the green parts of the plant, and in the plant complex organic compounds are synthesised from it. Because this process occurs only in the light the name of **photosynthesis** is given to it.

That the carbon is derived from the air may be shown in a number of ways, but most conveniently by means of water-culture experiments. In water-culture, plants are grown with their roots immersed in a solution of nutrient salts containing no carbon compounds. A suitable solution (after Sachs) for general work would be 1 grm. potassium nitrate, 0·5 grm. each of sodium chloride, calcium sulphate, magnesium phosphate and calcium phosphate, 2 drops (about 0·2 c.c.) of ferric chloride solution, and 1 litre of distilled water. Alternatively Knops' solution may be used.

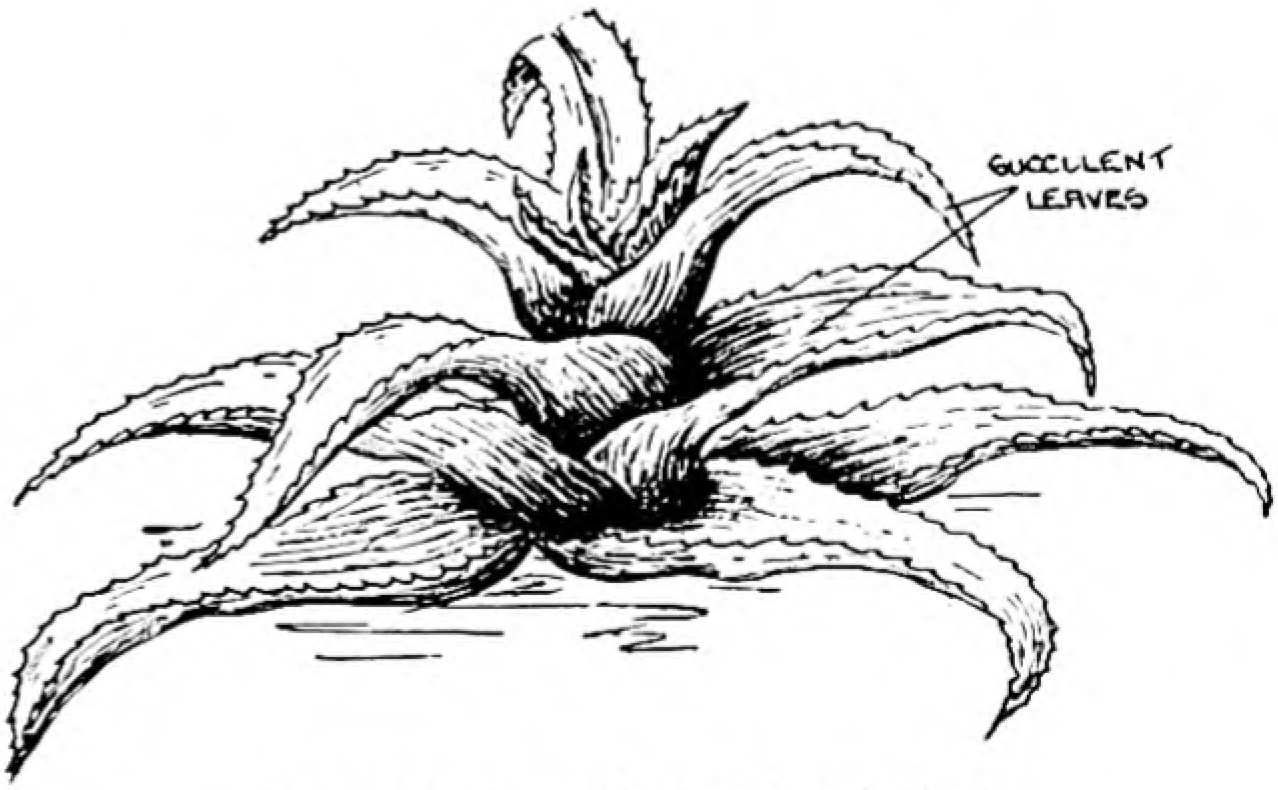


Fig. 140, A. *Aloe spinosissima.*

This consists of 0·4 grm. of calcium nitrate, 0·1 grm. each of potassium nitrate, magnesium sulphate, and potassium phosphate, with iron as before, dissolved in 1 litre of distilled water. These solutions make no provision for the supply of traces of boron, manganese, zinc, etc., but these are usually present in sufficient amount as impurities in the chemicals used for preparing the solution. The solution is placed in bottles of at least a litre capacity. Seedlings of any cereal, or of buckwheat (*Fagopyrum esculentum*), are grown in sand until the roots are a few centimetres long. They are then fixed into corks which are carried in the necks of the culture solution bottles in such a way that the roots of the plant are dipping into the solution. Alternatively rooted cuttings of *Bryophyllum pinnatum* or *Tradescantia virginiana* may be used. It is desirable to use sterilised bottles and to make provision for periodic aeration of the solution which should be renewed at least once every four or five weeks. The region of the stem which passes through the cork should be kept dry to prevent growth of mould. The bottles should be wrapped in dark paper to exclude light from the solution. If the temperature and illumination are satisfactory the plants in water-culture will exhibit normal growth, and it can be shown that in the process of growth their dry weight and content of carbon have increased. The culture solutions contain (and can supply to the plant) nitrogen, phosphorus, sulphur, iron, calcium, potassium, magnesium, hydrogen and oxygen (as water), but the only possible source of carbon is the atmosphere.

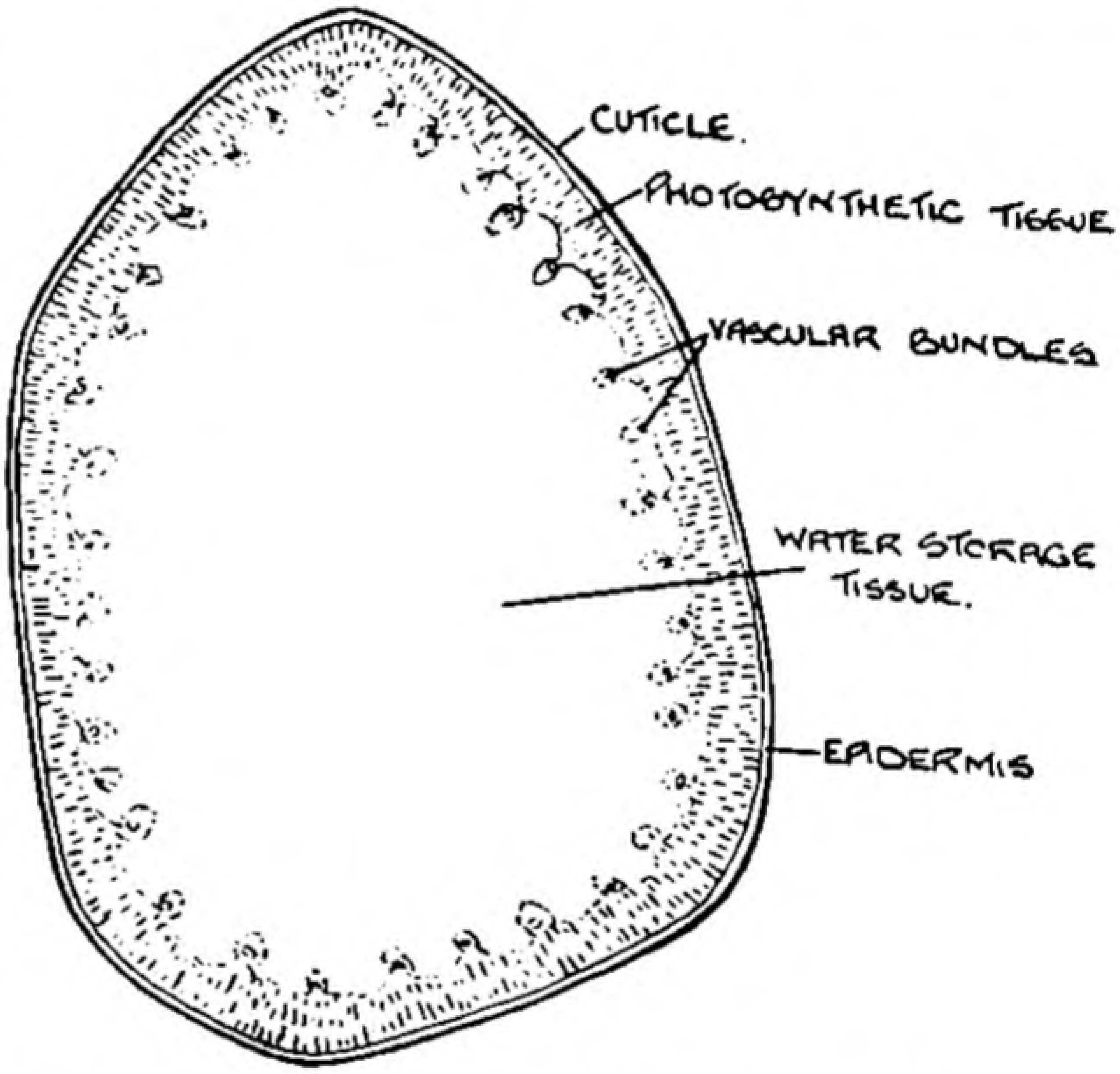


Fig. 140, B. *Aloe* LEAF, DIAGRAMMATIC TRANSVERSE SECTION, SHOWING CENTRAL WATER-STORAGE TISSUE.

In the atmosphere carbon dioxide is present only to the extent of three parts in ten thousand of air, but this carbon dioxide diffuses into the plant through the stomatal pores. It passes by diffusion into the intercellular spaces and dissolves in the water which saturates the cell-walls. It then diffuses in solution into the cells, and in the chlorophyll-containing cells such as the mesophyll of the leaf is elaborated into organic compounds.

19. The Products of Photosynthesis

The first easily demonstrable product of photosynthesis is usually starch. If a green leaf of *Hydrangea* or *Pelargonium* which has been growing in the light is killed by immersion in boiling water, placed in warm alcohol until it is decolourised and then floated out in iodine solution it assumes an intense blue-black colour, due to the presence in it of starch. The majority of leaves when tested in this way will be found to contain starch. Some Dicotyledons, e.g. *Gentiana*, and many Monocotyledons (*Allium*, *Scilla*, etc.), do not contain starch. Their leaves are usually rich in sugar.

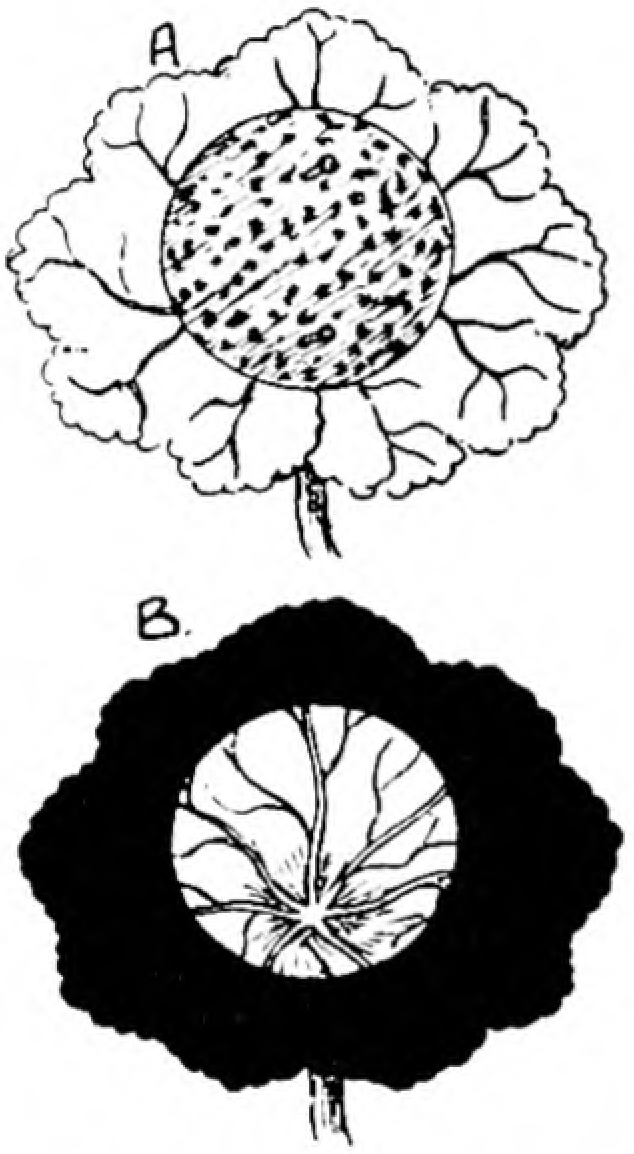


Fig. 141. Leaf-stencil Experiment, Photosynthesis.

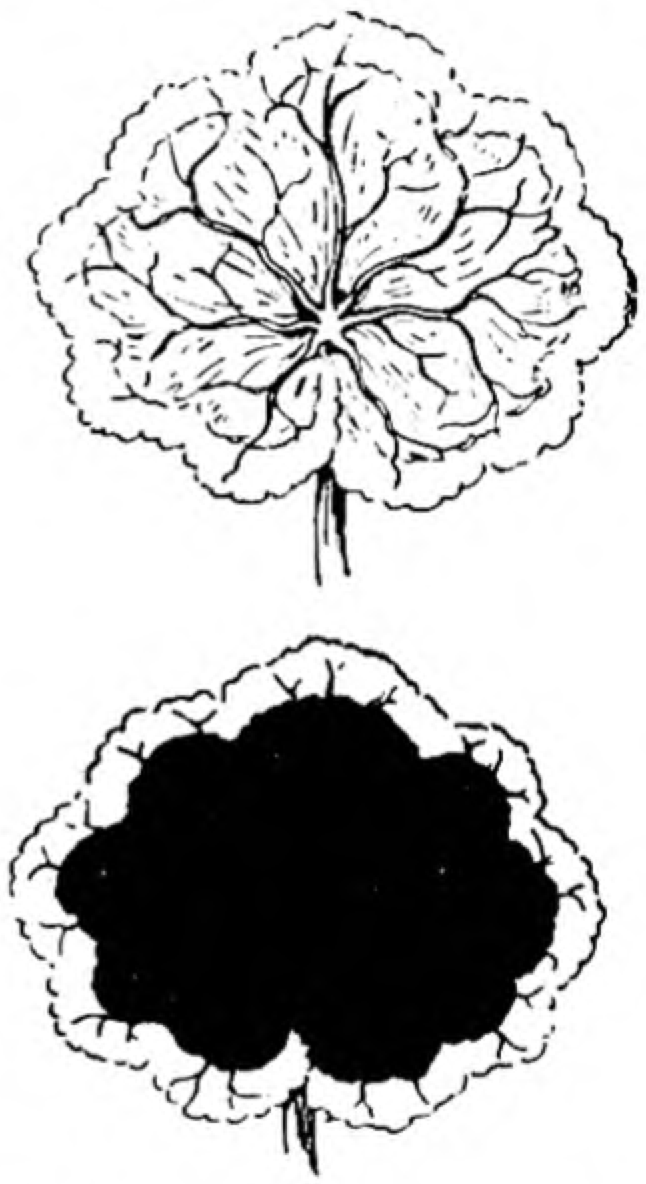


Fig. 142. Variegated Leaf, Photosynthesis.

If we keep a plant of *Pelargonium* in the dark for from twenty-four to thirty-six hours and at the end of this time test its leaves for starch, we find that they are starch-free and the plant is said to be de-starched. Such a de-starched plant when exposed to light rapidly forms starch in its leaves, and we might conclude, therefore, that the first product of photosynthesis is starch. Careful chemical analysis, however, shows that the synthesis of sugars precedes starch formation, and in the so-called "sugar leaves" sugar synthesis alone takes place.

20. Conditions Necessary for Photosynthesis

The fact that a de-starched plant when exposed to light rapidly synthesises starch in its green leaves suggests that light is essential to the process, and this is so. The synthesis of sugar or starch from carbon dioxide occurs only in the light. This can be demonstrated also by fixing to the leaf of a de-starched plant a stencil in such a way (Fig. 141) that only part of the leaf is illuminated. After a few hours exposure it will be found that starch synthesis has occurred only in the illuminated portions of the leaf.

Further, this synthesis takes place only in the presence of chlorophyll. If a suitable plant is kept in the dark for some days it will continue to grow, but the new leaves produced in the dark will remain yellow. With a few exceptions illumination is necessary for chlorophyll formation. If we expose this plant to light and then test its leaves for starch, we find that starch formation has occurred in the old green leaves, but not in the new yellow leaves. Chlorophyll, then, is necessary for photosynthesis. We reach a similar conclusion from a study of the process of photosynthesis in variegated plants (Fig. 142), where we find that photosynthesis occurs in the green, but not in the yellow or white regions of the leaves.

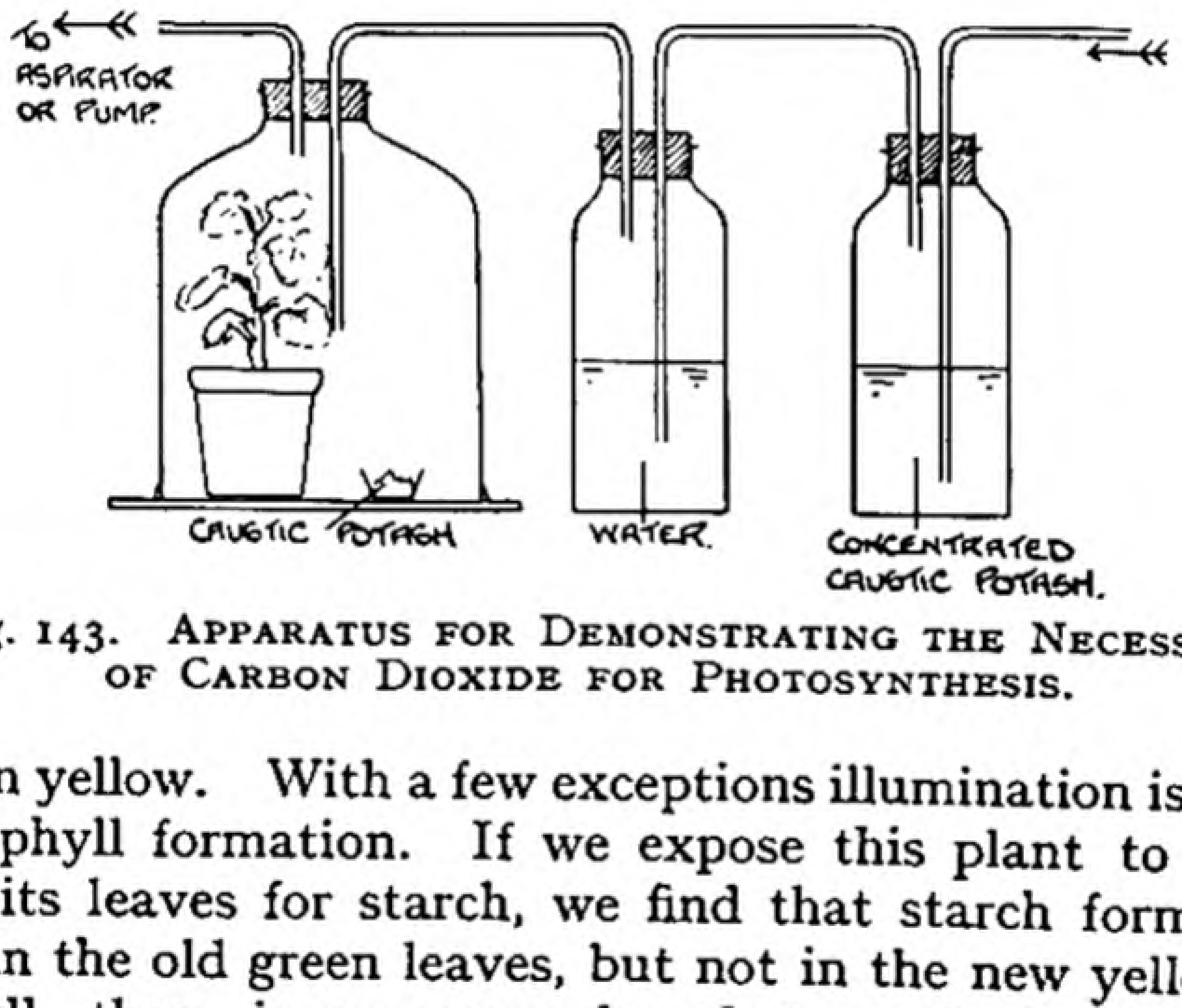


Fig. 143. Apparatus for Demonstrating the Necessity of Carbon Dioxide for Photosynthesis.

It is self-evident that photosynthesis cannot occur in the absence of a supply of carbon dioxide, but proof of this is afforded by keeping a de-starched plant in an atmosphere free from carbon dioxide (Fig. 143) and testing the leaves for starch. Under these conditions, although the illumination is satisfactory, the green leaves cannot synthesise starch. Photosynthesis, then, will occur in the green chlorophyll-containing cells of the plant provided these are illuminated and supplied with carbon dioxide.

21. Evolution of Oxygen during Photosynthesis

As long ago as the eighteenth century it was known that green plants possessed the ability to "purify" air which had become "impure" through the respiration of animals. It was known, too, that this purification occurred only when the green parts of the plant were exposed to light, and later it was shown that the purification was effected by the absorption of carbon dioxide and the evolution of oxygen by the green plant. Later investigations showed that the volume of oxygen evolved equals the volume of carbon dioxide absorbed, as indicated by the chemical equation

$$6\,CO_2 + 6\,H_2O = C_6H_{12}O_6 + 6\,O_2.$$

The demonstration of the evolution of oxygen by land plants is difficult. It involves gas analysis. With many water-plants the phenomenon can be demonstrated quite simply by the use of the apparatus shown in Fig. 144. Under the funnel is a number of shoots of the Canadian pondweed (*Elodea canadensis*) or other water plant. The funnel is immersed in water, or better still, a 0·1 per cent. solution of sodium bicarbonate, and a test-tube full of water inverted over the stem of the funnel. When the apparatus is illuminated the *Elodea* absorbs carbon dioxide from the solution, photosynthesis proceeds, and bubbles of gas may be seen issuing from the cut ends of the *Elodea* shoots. This gas collects at the top of the test-tube, and if subjected to ordinary chemical tests it will be found to be very rich in oxygen. It is not pure oxygen, but consists of a mixture of gases which have been displaced from the intercellular spaces of the plant. Oxygen is present, however, in greater proportion than in air.

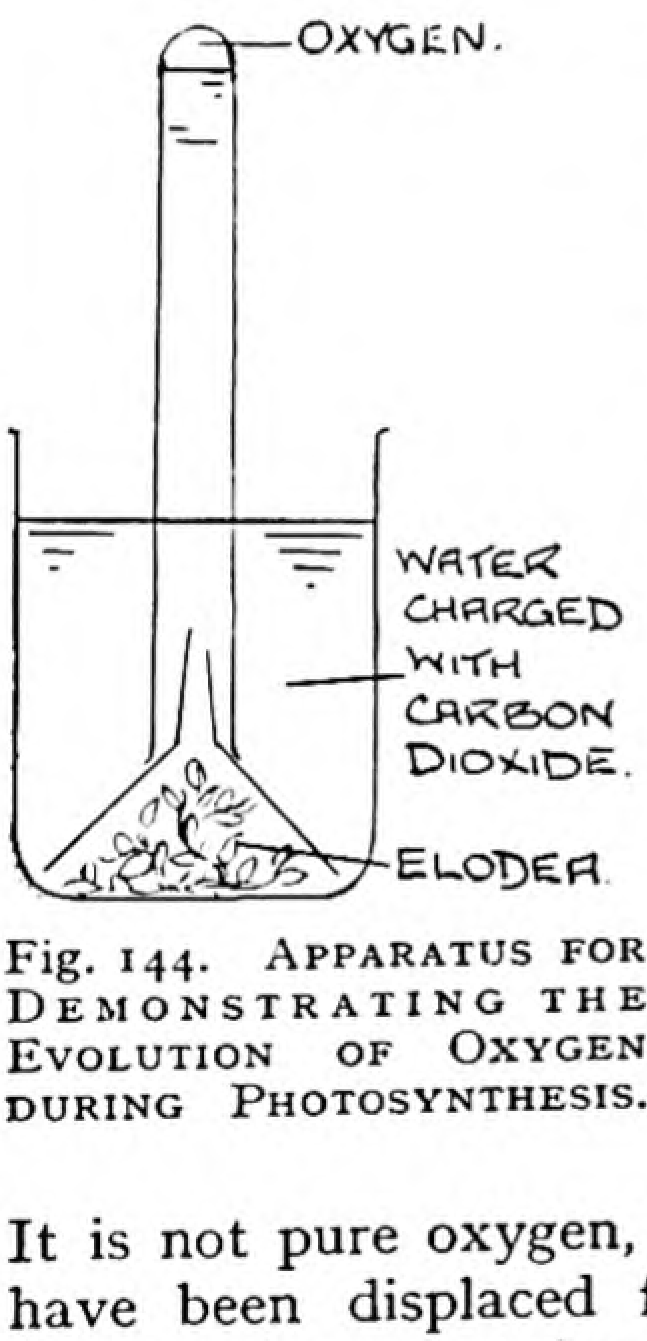


Fig. 144. Apparatus for Demonstrating the Evolution of Oxygen during Photosynthesis.

22. Mechanism of Photosynthesis

We have expressed the process of photosynthesis by the equation

$$6\,CO_2 + 6\,H_2O = C_6H_{12}O_6 + 6\,O_2.$$

It is unlikely that the synthesis of a sugar (glucose) occurs in one stage as shown in the equation. On theoretical grounds it would be expected that a reaction involving six molecules of carbon dioxide and six molecules of water would proceed at a rate so small as to be barely measurable. In fact, photosynthesis goes on rapidly, and this in itself provides evidence that it consists, not of a single chemical reaction, but of a whole chain of reactions. Further, as we shall see, in all probability one at least of these reactions can go on independently of light, so that photosynthesis consists of at least one " light reaction " and one " dark reaction."

A suggested mechanism of sugar synthesis is that formic acid is first formed, and that this is reduced to formaldehyde, which then polymerises to sugar, according to the equations

$$2\,CO_2 + 2\,H_2O = 2\,H.COOH + O_2$$
$$2\,H.COOH = 2\,H.CHO + O_2$$
$$6\,H.CHO = C_6H_{12}O_6$$

The occurrence of formaldehyde in green leaves has not yet been conclusively shown; but it is, of course, possible that its formation is followed at once by polymerisation. If this were so we should not expect to find appreciable amounts of formaldehyde in the tissues. Indeed, a rapid polymerisation of the formaldehyde would be a necessity as it is toxic to living cells. There are obvious difficulties in the way of acceptance of this mechanism of sugar synthesis, and we have to admit that the details of the process are very imperfectly understood. Neither do we know exactly where the sugar is synthesised. Observation shows that the starch grains which are ultimately formed are generally produced in or near to the chloroplast (see Fig. 7), and in view of the known importance of the chlorophyll it is believed that the chloroplast is the place in the cell where photosynthesis occurs. The formation of sugar in photosynthesis is generally followed by the production of starch, and this starch formation is governed by the concentration of sugar in the cell. When the sugar concentration reaches a certain critical level starch is produced. Even with some of the so called " sugar leaves " starch formation can be induced by floating them on sugar solution. Some sugar is absorbed, and the concentration of the sugar in the leaves is thus artificially increased to such an extent that starch forms.

It is interesting to note that this synthesis of starch from sugar can go on independently of both light and chlorophyll. It is in the synthesis of sugar from carbon dioxide that light and chlorophyll play an important part.

23. The Importance of Light

We have shown that photosynthesis goes on only in the presence of light. Sunlight consists of many different kinds of light rays, and we find by experiment that the green leaf synthesises carbohydrates from carbon dioxide most actively in blue and red light.

This is rather important because whereas diffuse light is rich in blue rays, direct sunlight is rich in red rays, and hence photosynthesis can take place both in diffuse and direct sunlight. The importance of light is that it supplies the energy necessary for the conversion of carbon dioxide into organic compounds. To convert six molecules of carbon dioxide into one molecule of glucose needs 674 thousand calories of energy, and this is supplied by the light. The chlorophyll provides the mechanism by which the light energy is made available for the process.

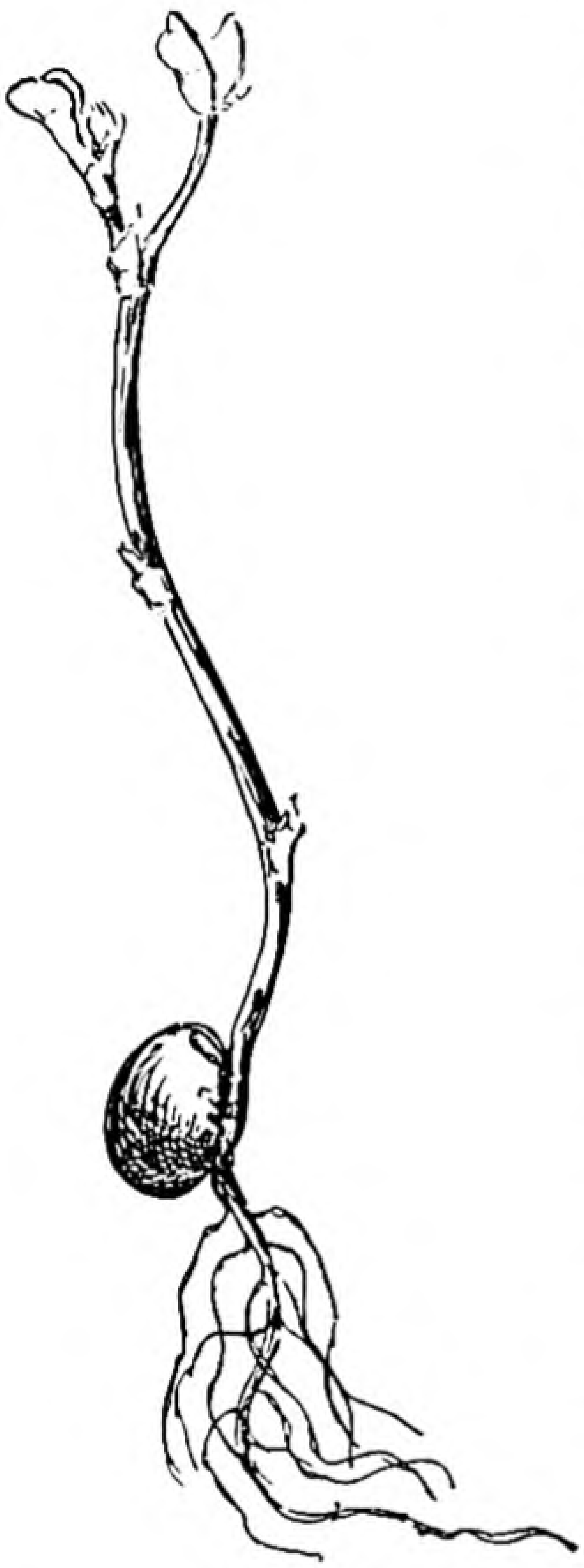


Fig. 145.

ETIOLATED BROAD BEAN SEEDLING GROWN IN DARK.

Note weak stem, elongated internodes and petioles, reduced laminae.

The energy thus absorbed is in reality stored in the products of the photosynthetic processes.

We shall see later (p. 191) that this energy may be released during the process of respiration, and then utilised for a variety of purposes. Organisms which do not possess chlorophyll, such as Fungi, Bacteria and animals, are also able to release and utilise this stored energy in their own life-processes (see pp. 196, 490 and 503).

24. Importance of Chlorophyll

We have already satisfied ourselves that photosynthesis is only possible in those tissues that contain chlorophyll. Chlorophyll is really a mixture of two green pigments, chlorophyll *a* and chlorophyll *b*, with the empirical formulae

$$C_{55}H_{72}O_5N_4Mg \text{ and } C_{55}H_{70}O_6N_4Mg.$$

Associated with the chlorophylls in the chloroplast are two yellow and orange pigments, carotene (a hydrocarbon) and xanthophyll. Only the chlorophylls are important in photosynthesis, and they are formed in the plant only under the influence of light. A plant grown in the dark remains devoid of chlorophyll; with the leaves yellow in colour, and the plant is said to be **etiolated.** The lack of light induces morphological peculiarities characteristic of etiolated plants—the internodes are abnormally long, the leaves small and rudimentary in character, whilst internally there is only a very feeble development of lignified tissue (Fig. 145). As we shall see later, chlorophyll only forms in the leaves when the plant has a supply of iron, although it is to be noted that iron does not enter into the chlorophyll molecule. Plants grown thus and lacking in iron are said to be **chlorotic,** and this condition of chlorosis, due to a nutritional deficiency, should be distinguished from etiolation brought about by the absence of light.

The pigments of the chloroplast can be extracted from the leaf by means of alcohol, and a rough separation of them is readily effected. The alcoholic extract is shaken with benzene and the two liquids allowed to separate. The upper benzene layer contains the chlorophylls whilst the alcohol layer contains the orange and yellow pigments. If a solution of chlorophyll is placed in the path of a beam of light which is then passed through a prism the spectrum is modified. Certain dark bands (absorption bands) appear in it, especially in the blue and red regions, because these particular rays have been absorbed by the chlorophyll. We have already seen that photosynthesis is most active in blue and red lights. This is because the chlorophyll absorbs these lights and harnesses their energy which is then made available for the process of photosynthesis. Only a small proportion (about 3%) of the light-energy falling on a leaf is absorbed in this way by the chlorophyll. Exactly how the light-energy absorbed is utilised, and the precise part that the chlorophyll plays in the process of photosynthesis are questions that still await elucidation.

25. The Rate of Photosynthesis

Innumerable measurements of the rate of photosynthesis have been made and we find that the rate varies with the plant employed, and is also dependent upon a variety of internal and external factors. On a bright sunny day a sunflower leaf will absorb about 13 c.c. of carbon dioxide per hour per 100 sq. cm. of leaf-surface. This, on conversion to a hexose sugar would yield 0·0165 grm. of carbohydrate. The photosynthetic rate, however, is very variable. Alterations in temperature affect its rate and within certain limits increase in temperature increases the rate of photosynthesis in just the same way as it increases the rate of other chemical reactions. Within the temperature limits of 0° C. and 25° C., a rise in temperature of 10° C. approximately doubles the rate of photosynthesis. But as the rise in temperature proceeds above a certain point, temporary damage to the protoplasm occurs and results in a fall in the photosynthetic rate. The extent of the decrease depends on the length of the period of exposure to the high temperature.

For example, in Fig. 146, A the "optimum" temperature depends partly on the periods over which the measurements of photosynthetic rate were made. The primary relation between temperature and photosynthesis is shown graphically in Fig. 146, B.

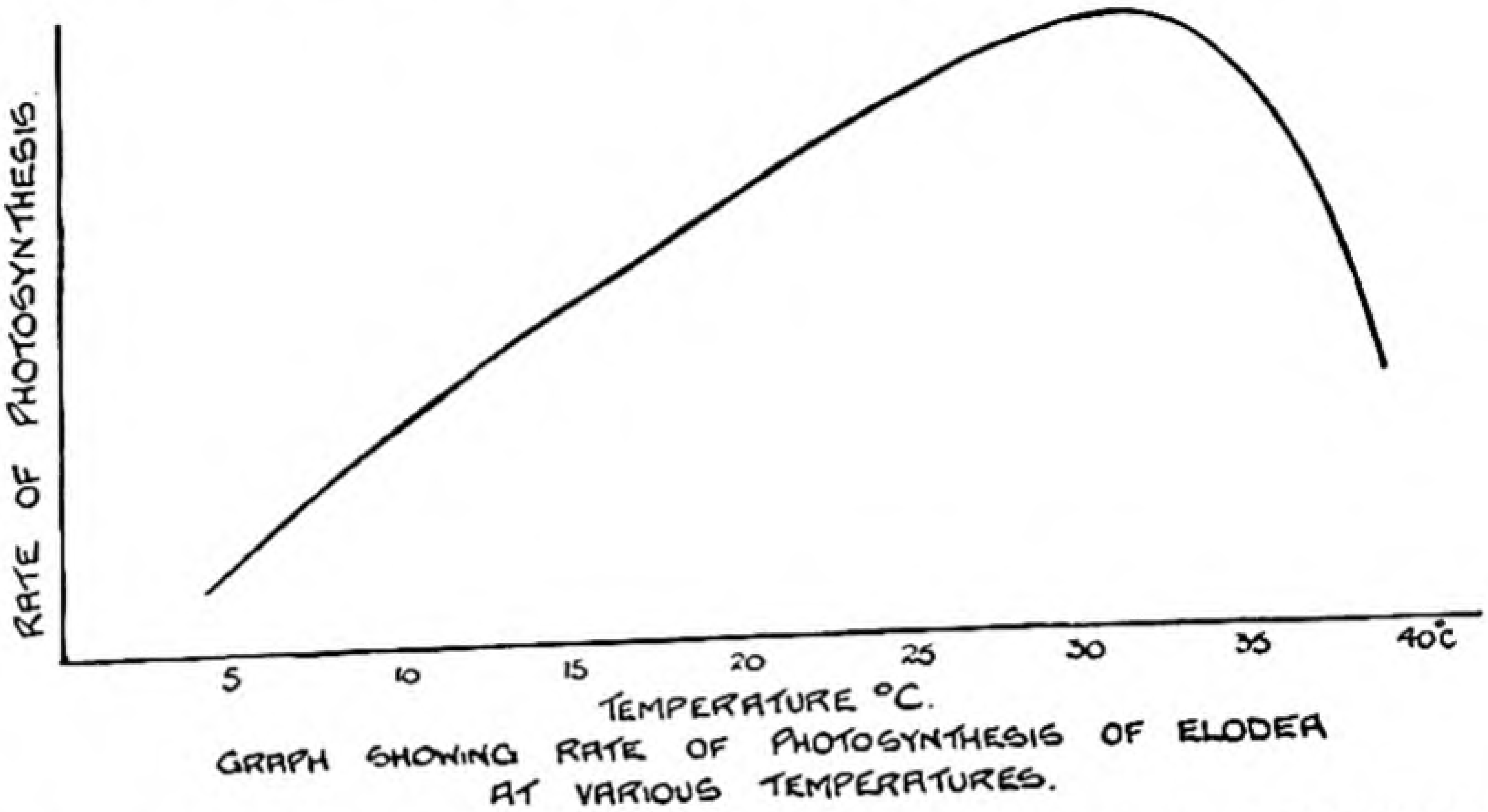


Fig. 146, A. Graph showing the Apparent Relation between Photosynthesis and Temperature.

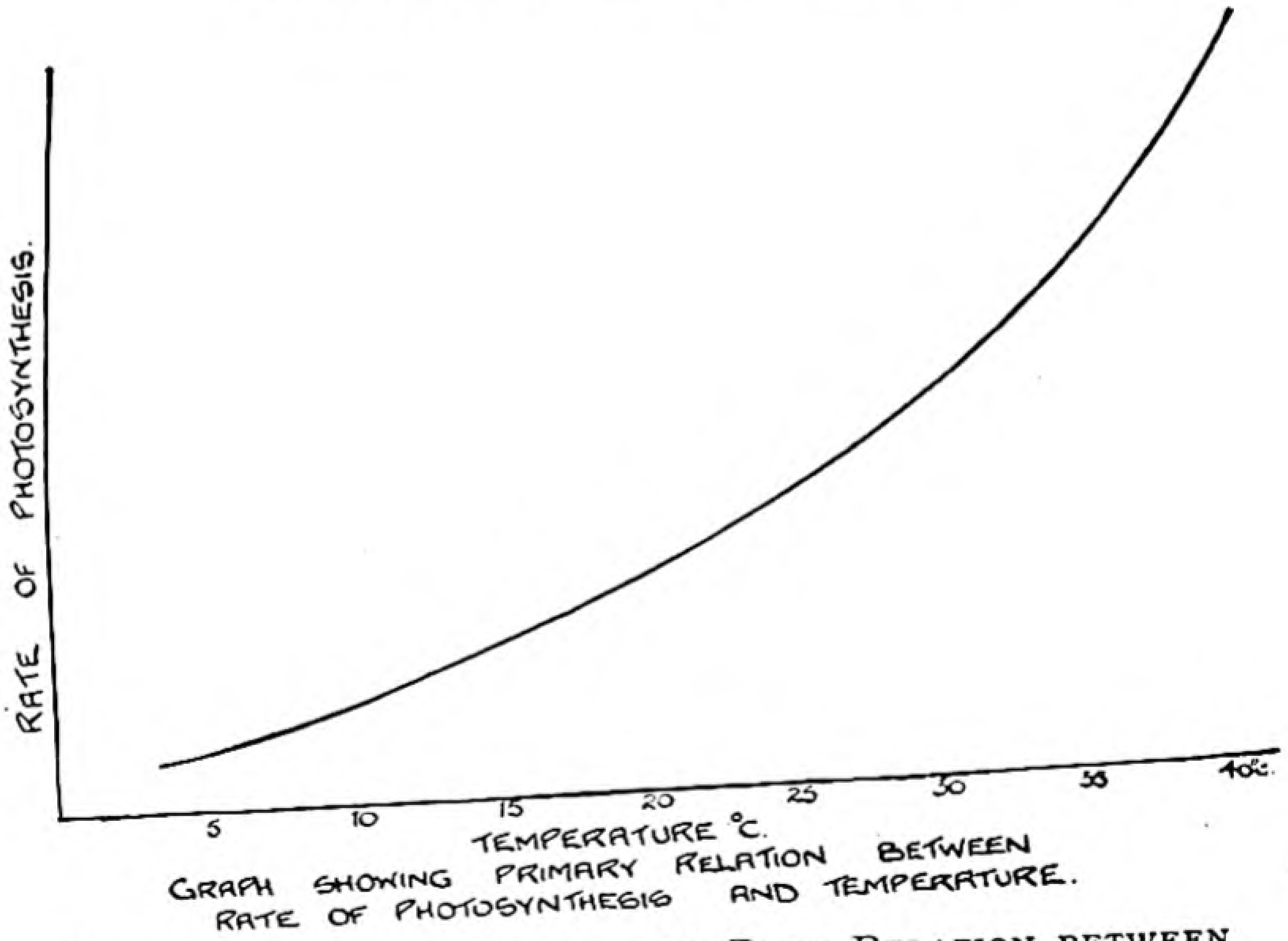


Fig. 146, B. Graph showing the Real Relation between Photosynthesis and Temperature.

Later on we shall have occasion to point out that many of the metabolic activities of the plant are affected in a similar way by temperature changes. Temperature increase, then, causes an increased amount of assimilation, but at high temperature the accelerating effect is more than counterbalanced by a decrease due to the protoplasmic damage if the exposure to the high temperature is prolonged. When we realise that photosynthesis is a photochemical reaction, it is surprising to find that increase in temperature has this accelerating effect. The rate of photochemical reactions is usually very little altered by temperature changes. This, then, constitutes further evidence that photosynthesis consists of at least one normal " dark " chemical reaction, in addition to the stages in which light plays an important part.

The intensity of illumination, and the supply of carbon dioxide too, affect the rate of photosynthesis. Experimentally we find that at very low light intensity, increase in the carbon dioxide supply has little effect on photosynthesis. Similarly if the carbon dioxide supply is very poor, increased illumination effects only a very slight increase in the rate of photosynthesis. At higher carbon dioxide concentrations and higher light intensities an increase in the amount of *either* factor may give an increased assimilation rate.

It may be noted that at very low light intensities photosynthesis is accelerated only slightly by temperature increases. When the light intensity is low it is the rate of the photochemical reaction, which is almost independent of temperature, that governs the rate of the whole process. We should remember, too, that it is not the concentration of carbon dioxide in the air (which can easily be measured), but the amount of carbon dioxide reaching the chloroplast which is important. Diffusion of carbon dioxide into the leaf takes place through the stomata, and hence will be restricted or cease when these close. Stomatal closure at night is of no importance in this respect because photosynthesis cannot go on in the dark. Stomatal closure, brought about by a water shortage, however, whilst it minimises the loss of water from the leaf, reduces the photosynthetic rate by reducing the inward diffusion of carbon dioxide.

26. Fate of the Sugar produced by Photosynthesis

The first carbohydrate formed as a product of photosynthesis is generally a sugar (glucose). If the sugar concentration is sufficiently high starch-formation occurs. The starch-formation which takes place in green leaves during the day can be looked upon as temporary storage of surplus carbohydrate. Storage of this surplus in the form of an insoluble substance has the obvious advantage that it does not affect the osmotic relations of the cell. During the night the temporary storage starch is reconverted into soluble sugars, which are translocated away from the leaf to other parts of the plant. They may then be used directly in the process of respiration or in growth (*i.e.* in the formation of new protoplasm and new cell-wall material), or be stored and utilised only at a later date.

The conversion of glucose into starch proceeds readily, but conversion of glucose into other carbohydrates also occurs, and as a result, many carbohydrates besides glucose and starch are found in the green leaf, and in other parts of the plant. Glucose can be converted into fructose. Then a molecule each of fructose and glucose may condense together to form sucrose, or several molecules of fructose may unite to form the polysaccharide inulin. The conversion of starch into glucose occurs in at least three stages. The starch first forms dextrin, then maltose, and finally glucose. This may explain the origin of the maltose sometimes found in plant material. Sugars with only five carbon atoms in the molecule (pentoses) and complex substances formed by the condensation of several pentose molecules (pentosans) are derived in some unknown way from the products of photosynthesis. The final product of photosynthesis in some lower plants (e.g. *Vaucheria*) is oil, and this is probably derived from the sugar which has been built up photosynthetically.

27. The Importance of Nitrogen and Mineral Salts

Early in the chapter it was pointed out that chemical analysis of plant material reveals that it contains not only oxygen, hydrogen, and carbon, but also nitrogen, chlorine, sulphur, phosphorus, potassium, sodium, calcium, magnesium, iron, manganese, silicon, iodine, copper, zinc and boron, in varying amounts. These elements are obtained from the soil. Water-culture experiments show that healthy growth of the plant is obtained if the culture solution contains magnesium, calcium, potassium and iron in the form of nitrates, phosphates and sulphates. It would appear, therefore, that only these elements are essential to the plant. If, however, we carry out water-culture experiments in which the very purest chemicals (spectroscopically pure) and distilled water are used, and special precautions taken to prevent the solution of even minute traces of material from the walls of the containing vessel, then we find that some plants do not thrive unless they are supplied with traces of manganese, zinc, copper and boron. Only traces of these elements are necessary. High concentrations are toxic. Clearly then, although silicon, sodium and chlorine are present in plant tissue they are not essential to the plant. The other elements enumerated are essential. Their essential nature is indicated by the unsatisfactory growth of a plant if its roots are immersed in a solution lacking any one of them. By observing the behaviour of plants deprived of a supply of one element but supplied with all the others we gain an insight into the function performed by these elements in the plant. Although these elements are essential, the amount of them present in the plant is not large. The mineral salts left behind as ash when plant material is incinerated often constitute only three or four per cent. of the dry weight, although much more may be present, especially in leaves.

Not only must a supply of all the essential elements be available to the plant, but they must be supplied in suitable proportion. We find, for instance, that although calcium is essential, a solution of calcium salts, containing nothing else, is toxic. Similarly, magnesium alone may be toxic, but magnesium and calcium when supplied together no longer exert a toxic effect. A solution in which all the essential elements are present, and present in such proportions that they do not exert toxic effects, is called a physiologically balanced solution.

28. Functions of Nitrogen and Mineral Salts

Nitrogen, sulphur and phosphorus are constituents of proteins, and when we remember that proteins are contained in the living protoplasm the essential nature of these elements will be realised. All proteins contain nitrogen, but phosphorus-containing proteins seem to be especially abundant in the cell nucleus. Nitrogen and magnesium are constituents of the chlorophyll molecule. Only a small amount of magnesium is used in this way, however, and a supply of magnesium greatly in excess of the magnesium needed for chlorophyll synthesis appears to be essential. Chlorophyll development is retarded or prevented if the supply of iron is deficient. Although the chlorophyll molecule contains no iron its synthesis depends on a supply of iron. Iron-starved plants, because of the failure of chlorophyll synthesis, are typically pale or even yellow; a condition spoken of as **chlorosis.** Potassium starvation usually brings about a disturbance of the water relations of the plant, resulting in a withering of the apices and margins of the older leaves. Unless the supply of potassium is adequate the rate of photosynthesis may be less than normal. Potassium deficiency may induce chlorosis, and this condition sometimes results from a deficiency of sulphur (e.g. in rice and tea). In spite of its importance and its abundance in those regions of the plant where growth is most active, potassium is not, as far as is known, a constituent of any essential organic substance in the cell. Probably this is true of calcium also. In the absence of a supply of calcium the roots may lack their normal firmness, probably owing to disorganisation of the middle lamellae of the cell-walls.

Much of the calcium of the plant is present in the form of insoluble crystals of calcium oxalate, carbonate or sulphate, and here the calcium may function by removing from solution unwanted and possibly toxic substances. Chlorophyll development is disturbed and chlorosis may develop if the supply of manganese is inadequate, whilst in oats manganese deficiency results in a spotting of the foliage. Boron and copper are certainly essential for some, if not all plants, but the functions of these and other " trace " elements are but imperfectly understood.

It is important to note that the absence of a particular element often results in the development of characteristic and well defined symptoms in the plant, and by a study of these, nutritional deficiencies of crop plants can often be diagnosed.

29. Supply of Nitrogen and Minerals

The minerals present in the soil solution have their origin in the weathering of the rock fragments that form the mineral skeleton of the soil. The mineral substances in solution suffer certain losses by drainage. The amount lost in this way is not so great as might be imagined as the colloids of the soil, both humus and clay, adsorb some ions. Potassium especially is held in this and other ways, whereas calcium washes out more or less readily. The nitrogen of the soil is not derived from the rock fragments. Some nitrogen compounds reach the soil in rain, having been formed by the combination of nitrogen and oxygen as a result of lightning flashes in the air. Certain soil Bacteria are able to synthesise nitrogen compounds from gaseous nitrogen, and the amount of combined nitrogen present in the soil is increased by this method. The greater part of the combined nitrogen is present in the soil in the form of organic nitrogenous compounds. These cannot be absorbed by the roots of green plants, and so complex nitrogen compounds synthesised by soil Bacteria and nitrogenous material returned to the soil in dead plant and animal remains do not form a direct source of nitrogen for the green plant. By bacterial action these compounds are broken down first to ammonium compounds and finally to nitrates. The nitrates form the source from which green plants derive their nitrogen. Some plants may absorb ammonium salts, but more complex nitrogen compounds are not absorbed. Nitrates are readily washed out of the soil, but bacterial activity, by promoting the breakdown of complex nitrogen compounds, maintains in the soil a supply of nitrates.

Under natural conditions all the nitrogen and minerals absorbed from the soil are returned to it either directly or indirectly in the form of dead plant and animal remains and excreta. Hence the soil is not depleted of these substances except by drainage losses. When crops are removed there is a removal of the minerals and nitrogen that the plants had absorbed. These losses can be made good, and the fertility of the soil maintained, by manuring.

30. Absorption of Nitrates and other Salts by the Plant

Water-culture experiments offer a sufficient proof that a whole range of inorganic substances can be and are absorbed from solutions by the cells of a plant. We have many times stressed the fact that the cytoplasm of the cell forms a semipermeable membrane which allows the passage of water, but is impermeable to most dissolved substances. If the membrane were permeable to these solutes the phenomenon of plasmolysis would not take place. Further, the concentration of inorganic substances in the cell-sap of a root-hair is usually greater than that in the soil solution. If, therefore, free diffusion of inorganic solution across the cytoplasmic membrane could occur, we should expect to get an outward diffusion of salts from the root-hair rather than an absorption of salts by it. In fact, the movement of salts is from the weak soil solution to the more concentrated cell-sap, and would appear to be against the laws of diffusion. This accumulation of salts by plant cells is most marked when the supply of oxygen is good, and when respiration and protein synthesis (p. 187) are most active, and is probably conditioned by these processes. It is important to realise that the salts enter the cell as ions and not in the form of molecules. To show this we have only to immerse discs of tissue cut from a potato tuber in a dilute solution of potassium chloride, when we find that the potassium and the chloride are absorbed at different rates.

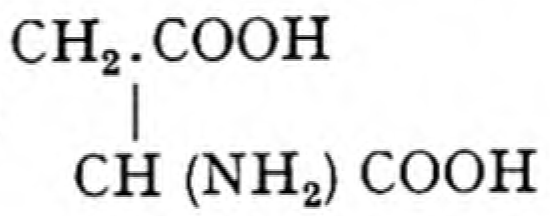
The difficulty of postulating a scheme which explains satisfactorily the entry into, and accumulation by, a cell of inorganic salts does not extend to all types of absorption. Especially with some organic substances, ease of entry into the cell is related to molecule size, alcohol, with a small molecule, entering the cell more readily than glycerol. In many such cases, too, the absorption seems to follow the ordinary laws of diffusion, continuing until the concentrations on the two sides of the membrane are equal.

31. Nitrogen Metabolism

A wide variety of nitrogen compounds occur in plant material. Basic substances such as the alkaloids and glycosides are of limited distribution, and with functions not clearly understood. Chlorophyll is present in green tissues and its importance has been pointed out. Amino acids, and amides are often abundant and probably represent stages either in the synthesis or breakdown of proteins, colloidal substances, which form the basis of the protoplasm, and form a store of food in many seeds. Nitrates and ammonium salts occur in plant material too, but their amount is usually small. The all important proteins are believed to be built up from amino acids. The simplest amino acid is glycin or amino acetic acid, $CH_2\ (NH_2)\ COOH$. This has an acid radicle—$COOH$, and a basic radicle—NH_2, and hence is able to combine with both acidic and basic substances. An amino acid, therefore, is able to combine with other amino acids, the NH_2 group of one molecule combining with the $COOH$ group of another with the elimination of water. In this way compounds of varying complexity may be built up, according to the number of amino acid molecules linked. It is in this manner that compounds of the type known as polypeptides, and finally proteins, are formed. Some of the commonest amino acids which it is known may enter into the constitution of the protein molecule are

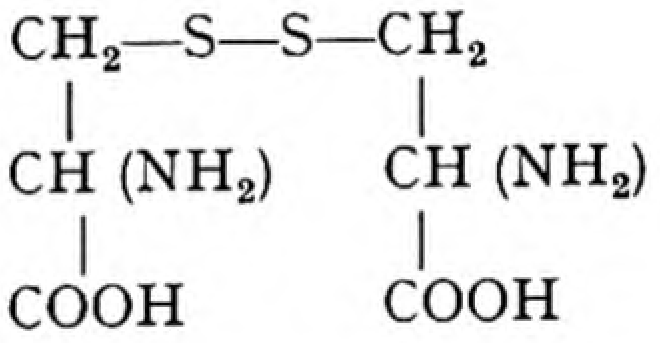
Amino-propionic acid $CH_3CH\ (NH_2)\ COOH$.

Aspartic acid



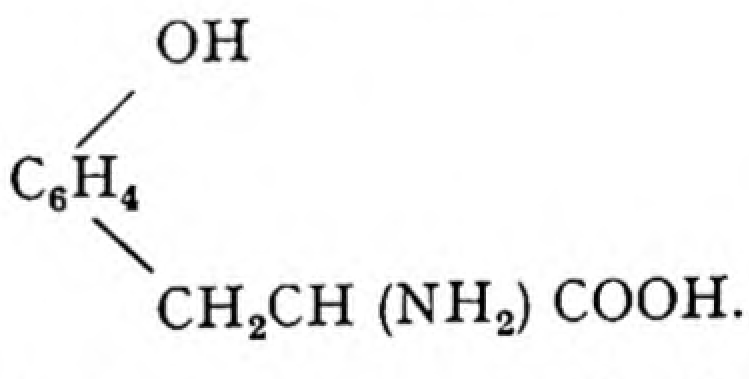
$$\begin{array}{l} CH_2.COOH \\ | \\ CH\ (NH_2)\ COOH \end{array}$$

Cystine



$$\begin{array}{ll} CH_2\text{—}S\text{—}S\text{—} & CH_2 \\ | & | \\ CH\ (NH_2) & CH\ (NH_2) \\ | & | \\ COOH & COOH \end{array}$$

Tyrosine



This by no means exhausts the list of amino acids which may go to build up molecules of plant proteins. A great number of amino acids may be utilised, and so the possible types of combination and hence the possible number of kinds of protein that may be formed is almost infinitely large. The proteins, though they may differ in solubility and other physical attributes, and in chemical composition, have many features which they always exhibit. The protein molecule is large and so exerts for a unit weight of protein, a small osmotic pressure. The molecule exhibits both basic and acidic properties and its physical condition is easily affected by temperature changes and changes in acidity. It has colloidal properties, imbibes water readily and swells, and some of these characters of the protein molecule are important in that they help to determine the physical characters of the protoplasm of which the proteins form a part. One of the changes in the protoplasm which occurs at death is probably the "coagulation" or precipitation of its colloidal proteins.

32. Synthesis of Organic Nitrogen Compounds

The nitrogen which is present in the proteins of the plant has been absorbed in the form of nitrates by the roots from the soil solution.

The nitrate so absorbed can rarely be detected in more than traces in the aerial parts of the plant, and so it is evident that transformation of nitrates into organic compounds may take place in the roots. We conclude, therefore, that in this process light and chlorophyll do not play an important part. Sometimes nitrates do accumulate in foliage leaves, but this probably represents a surplus of nitrogen that has been absorbed over and above the requirements of the plant. It is unlikely that the plant can transform nitrates directly into the amino acids necessary for protein synthesis. It is more likely that the nitrates are first converted to nitrites and then ammonium compounds. These by interaction with organic acids may give rise to amino acids and probably amides, and from these substances proteins may be synthesised. It is not certain that all the amino acids and amides of the plant arise in this way. They may also be produced by protein breakdown, and having been formed in this way, may break down further to form ammonia. The steps in protein metabolism which we envisage then are:—

$$\begin{tikzcd}
\text{Nitrate} \arrow[r] & \text{Nitrite} \arrow[r] & \text{Ammonia} \arrow[r] & \text{Amino Acids and Amides} \arrow[r] & \text{Protein} \arrow[dl] \\
 & & & \text{Amino Acid and Amides} \arrow[ul] &
\end{tikzcd}$$

Some of the chemical reactions involved in protein synthesis are endothermic, and therefore need a supply of energy. This is obtained by the oxidation of carbohydrates in respiration (see p. 191), and hence protein synthesis will go on most actively when and where the carbohydrate supply is good. We must point out, too, that organic acids, utilised in the synthesis of proteins, have their origin in the carbohydrates of the plant.

33. Transport of Food Materials

Water and mineral substances absorbed by the roots are, as we have seen, transported in the xylem to the transpiring organs of the plant. The carbohydrates of the plant are synthesised from carbon dioxide and water in the green cells of the plant. In soluble form (*i.e.* as sugars) they are then transported to other parts of the plant, and either used directly, or stored and utilised at some future time. This transport of soluble carbohydrates from the seat of photosynthesis takes place through the phloem and more especially in the sieve-tubes. The process is one analogous to, but not identical with, diffusion, and it is not clear what part the living protoplasm of the sieve-tubes takes in the transport. The sieve-tubes, too, form the channel in which complex nitrogen compounds are transported. Although the primary upward transport of minerals occurs in the xylem, there may be movement of mineral salts from leaf to leaf or from leaf to growing point through the phloem. The importance of the phloem in food transport is shown by ringing experiments. By means of an experiment of this type (Fig. 123) we have already shown that upward movement of water in the plant occurs in the xylem. If a ringed plant which has been exposed to the light is subjected to chemical analysis it is found that there is no downward transport of carbohydrates and proteins across the ring. We conclude, therefore, that this transport normally occurs through some tissue external to the xylem. The channel for this transport is in fact provided by the sieve-tubes of the phloem.

34. Storage and Reserve Materials

Photosynthesis usually proceeds during the day at such a rate that all the products are not removed from the leaf immediately. The surplus is converted to starch, which is retransformed into sugar and transported from the leaf during the night. All the carbohydrate removed from the leaf in this way is not utilised at once by the plant. A considerable proportion is stored, especially in the cortex of the root, and in trees and shrubs in the medullary rays of the shoot. It may be stored in special storage organs, e.g. bulbs, corms, tubers, swollen roots, etc., and when seed-formation is occurring food-material passes to the seed to form a store of food there. Reserve food-material, whether carbohydrate, fat or protein, is generally either in solid form, or consists of substances with a high molecular weight, which therefore exert a low osmotic pressure. Substances most frequently met with as reserve materials are

1. CARBOHYDRATES
    - (*a*) Starch in the form of starch-grains in potato tubers, cereals, etc.
    - (*b*) Sucrose in solution in the cells of the onion bulb, beetroot, etc.

(*c*) Glucose in solution in the cells of carrot.

(*d*) Inulin in solution in the cells of *Dahlia* and Jerusalem artichoke tubers.

(*e*) Hemicelluloses; a special form of cellulose, found in the seeds of lupin, coffee, nux vomica and date.

2. FATS AND OILS in many seeds (e.g. *Helianthus* (sunflower), *Ricinus* (castor bean) and many " nuts ").

3. PROTEINS, either in soluble or " crystalline " form, e.g. aleurone grains in *Ricinus* seeds.

35. Enzymes

The storage or reserve materials generally consist of insoluble substances, e.g. starch. Before these substances can be utilised they must first be brought into solution. Only then can they be transported from the region of storage to those parts of the plant where they are to be utilised. The conversion of starch to soluble sugar can be effected readily in the laboratory by more or less prolonged boiling with dilute acids. The process is one of hydrolysis, e.g.

$$(C_6H_{10}O_5)n + nH_2O = nC_6H_{12}O_6$$

and the acid catalyses the reaction.

A similar hydrolysis of starch and glucose takes place in the plant. The reaction here takes place at ordinary temperatures and is catalysed not by an acid but by an enzyme. Enzymes are organic colloidal catalysts produced by the activity of the protoplasm. They are not themselves living, and preparations possessing enzyme activity may be readily obtained from plant material. In the hydrolysis of starch to glucose more than one enzyme is involved. But the same enzymes which catalyse the hydrolysis of starch to glucose also catalyse the synthesis of starch from glucose.

The enzyme reactions are reversible and the same enzyme catalyses both the forward and back reactions. Enzymes are usually specific and the enzyme which, for instance, catalyses the hydrolysis of sucrose to glucose and fructose is without effect on starch. Some of the more important plant enzymes, together with the substance whose hydrolysis they catalyse, and the products of these hydrolyses are shown in the table on p. 190.

ENZYME	SUBSTANCE	PRODUCTS
Diastase	Starch	Dextrin
Dextrinase	Dextrin	Maltose
Maltase	Maltose	Glucose
Invertase	Sucrose	Glucose and fructose
Inulase	Inulin	Fructose
Cytase	Hemicellulose	Mannose and galactose
Glycosidases	Glycosides	Sugar and other substances
Lipase	Fats and oils	Glycerol and fatty acids
Urease	Urea	Ammonia and carbon dioxide
Peptases	Proteins	Peptone
Eryptases	Peptones	Amino acids

All plant enzymes are not concerned with hydrolyses. There are also oxidising enzymes, which fall into three main groups—oxidases, peroxidases and dehydrases. Oxidase is a term applied to an enzyme system, present in many plant cells, which, in the presence of molecular oxygen gives a blue colour with guaiacum resin. This is due to the oxidation of one of the constituents of the resin. Oxygen alone does not bring about this oxidation. It is effected only in the presence of oxidase. Peroxidases bring about the oxidation of many phenolic compounds in the presence of hydrogen peroxide, but not of molecular oxygen. Probably the peroxidase catalyses the decomposition of the hydrogen peroxide into water and atomic or nascent oxygen, and this " active " oxygen oxidises the phenolic compound. Tissues containing peroxidase but not oxidase will oxidise constituents of guaiacum resin only when hydrogen peroxide is present. Dehydrases generally bring about oxidation by the removal of hydrogen.

Another type of enzyme is the nitrate-reducing enzyme, which reduces nitrate to nitrite in the presence of aldehyde. The aldehyde is oxidised to the corresponding acid. Enzymes of this type, where the enzyme action involves an oxidation and a reduction, are sometimes called oxido-reductases. *Zymase* is the name given to what was formerly thought to be a single enzyme, but is now known to be a whole complex of enzymes which bring about the fermentation of certain sugars with the production of ethyl alcohol and carbon dioxide. The zymase enzyme-complex is especially abundant in yeast cells, but is found also in the tissues of other plants. Enzymes are important in plant metabolism because they catalyse reactions within the plant cells. It is important to realise that they can function independently of the plant. Generally, enzymes show a close parallel to other catalysts in that they do not appear in the equation representing the reaction; they catalyse but do not initiate chemical reactions, and the amount of chemical change that occurs is more or less independent of the amount of enzyme present. Many catalysts are inactivated or poisoned by such toxic substances as hydrogen sulphide, hydrocyanic acid and many arsenic compounds. Enzymes are similarly affected by these substances.

Enzymes are colloidal organic substances. At moderate temperatures (e.g. below 60° C.) the catalytic effect of the enzymes is increased by a rise in temperature. At temperatures much higher than this the enzyme is inactivated, probably owing to alteration of its colloidal nature. The destruction of enzymes by heat does not occur except at temperatures somewhat higher than those at which the living protoplasm is damaged. Hence high-temperature damage to enzymes is unlikely to occur within the living plant.

36. Anabolic Processes

We have considered so far mainly the anabolic processes which go on in the green plant. Under this heading we include the building up of carbohydrates, fats and proteins. From these, new protoplasm, new cell-walls, etc., are synthesised, and so the production of new tissues becomes possible. Most of the reactions involved in these anabolic processes are endothermic. The energy necessary for these actions may be derived from an outside source, as with photosynthesis, or it may be derived from the katabolic or breaking down processes which go on in the living organism.

37. Respiration

Respiration is a process which takes place in every living cell. It is essentially a katabolic process involving typically the oxidative breakdown of organic material. The oxidation generally takes place at the expense of oxygen absorbed by the cell, and carbon dioxide is generally one of the products of the breakdown. In the green land plant the necessary oxygen enters the plant mainly through the stomata and lenticels and diffuses throughout the intercellular spaces, finally passing into the cells in solution. The carbon dioxide liberated during the process is usually equal in volume to the oxygen absorbed. If for a moment we assume that a sugar (glucose) is the substance oxidised we can represent the process by the equation

$$C_6H_{12}O_6 + 6\ O_2 \rightarrow 6\ CO_2 + 6\ H_2O + 674\ \text{Calories.}$$

We see that the oxidation results in the liberation of energy and the process is the exact reverse of photosynthesis. In the green cells both photosynthesis and respiration go on, and which predominates depends on the light intensity. The light intensity at which the loss of sugar by oxidation is exactly equalled by the amount of sugar synthesised is spoken of as the compensation point.

The chief points of distinction between respiration and photosynthesis are:—

	Respiration	Photosynthesis
1.	A katabolic process associated with the breakdown of organic matter.	An anabolic process associated with the synthesis of organic matter.
2.	Takes place in all living cells.	Is confined to chlorophyll-containing cells.
3.	O_2 is absorbed. CO_2 liberated.	CO_2 absorbed. O_2 liberated.
4.	Independent of light.	Dependent on light.
5.	Energy is liberated.	Energy is absorbed.

The rate of respiration varies very much according to the activities of the cells. Actively growing tissues such as those of germinating cress seeds may, as the result of respiration, evolve 80 c.c. of CO_2 per gram of dry weight per day. With actively growing Fungi the amount of CO_2 evolved may be as much as 1800 c.c. per gram of dry weight per day. With relatively inactive tissue such as those of dry seeds the rate is naturally much less. The rate of respiration is influenced, too, by temperature. The relation between temperature and respiration rate is similar to that between temperature and photosynthesis (see p. 180 and Fig. 146). The primary effect of an increase in temperature is an increase in the rate of respiration. For a rise in temperature of 10° C. the rate is approximately doubled. At temperatures much above 35° C. there is a secondary effect. Prolonged exposure to these higher temperatures results in damage to the protoplasm and the respiration rate falls.

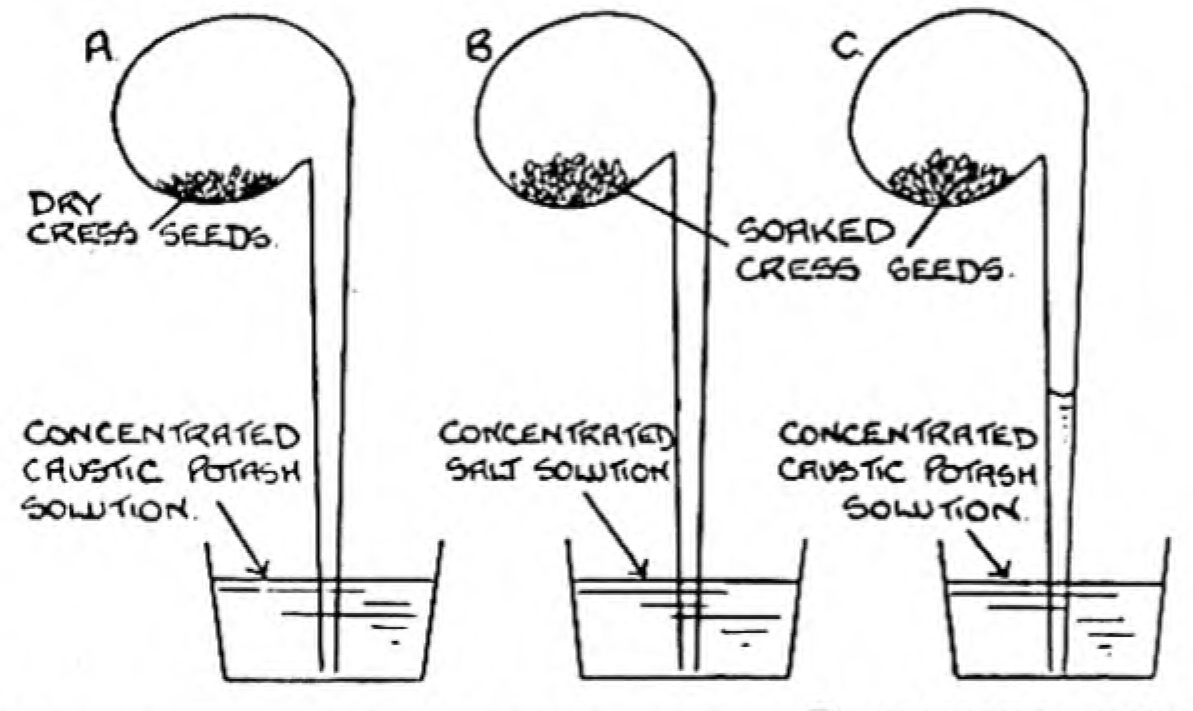

A
B
C
DRY CRESS SEEDS
SOAKED CRESS SEEDS
CONCENTRATED CAUSTIC POTASH SOLUTION
CONCENTRATED SALT SOLUTION
CONCENTRATED CAUSTIC POTASH SOLUTION

Fig. 147. Apparatus for Demonstrating the Evolution of Carbon Dioxide by Germinating Seeds.

The evolution of carbon dioxide from living plant material can readily be demonstrated by the use of the simple apparatus shown in Fig. 147. Here the three retorts, A, B, and C

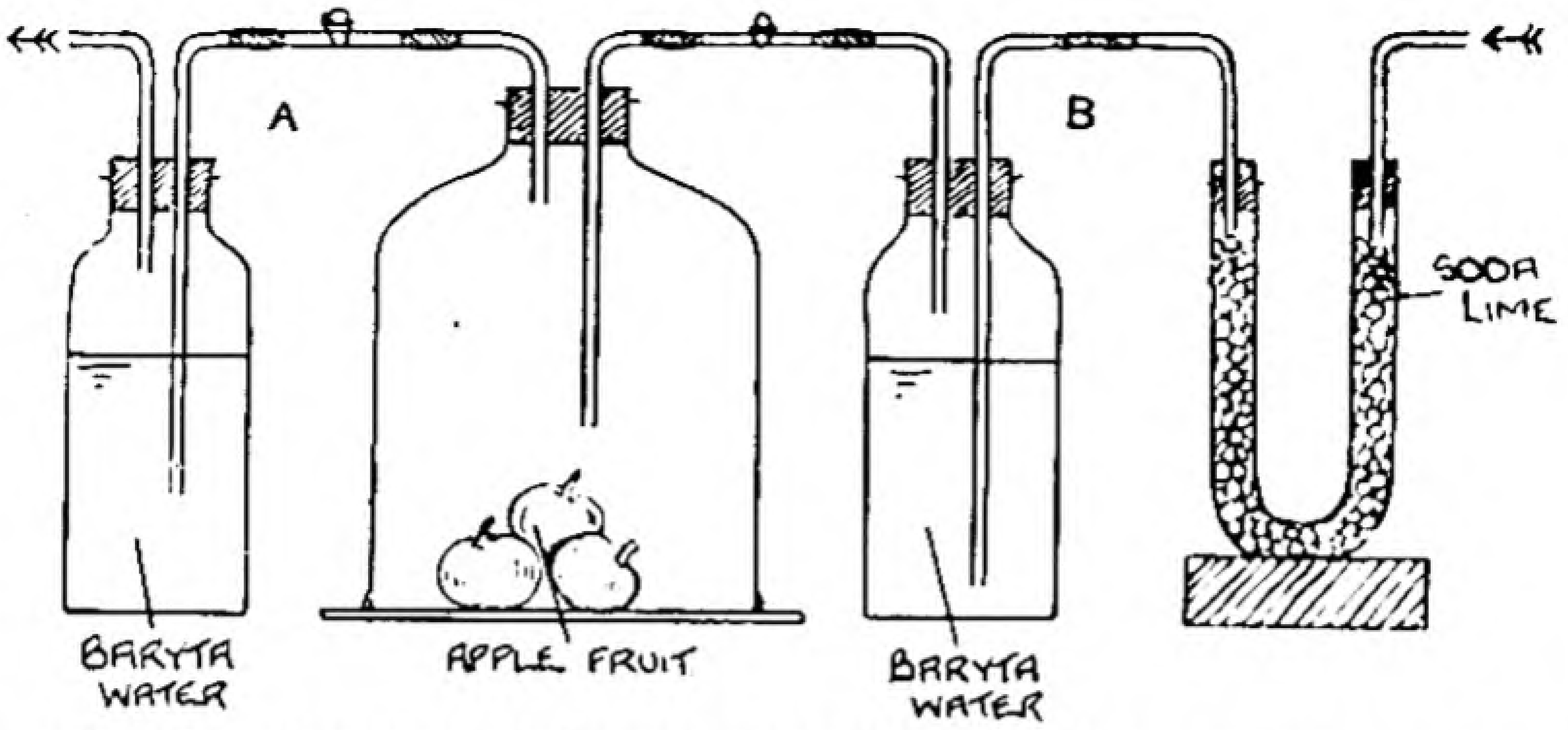


Fig. 148. Apparatus for Demonstrating the Evolution of Carbon Dioxide during Respiration.

contain cress seeds. In A the cress seed is dry. B and C contain cress seed which has been soaked in water. The ends of the retorts A and C dip into strong caustic potash and the end of retort B into concentrated brine. In A and B the levels of the liquids remain constant. In C the liquid rises in the retort. The dry seeds in A are relatively inactive and the gaseous exchange they undergo is too small to have any noticeable effect on the total volume of the gas in the retort. The soaked seeds in C respire vigorously, taking in oxygen from the air in the retort. The carbon dioxide liberated is absorbed by the caustic potash into which the retort dips. Hence the total volume of gas in the retort diminishes and the level of the potash rises. In B oxygen absorption and carbon dioxide evolution also occur, but the end of the retort dips into strong brine, in which oxygen and carbon dioxide are both only very slightly soluble. The level of the liquid here remains unchanged, an indication that the volumes of oxygen absorbed and carbon dioxide liberated by the cress seed are equal.

The above demonstration is satisfactory only so long as no violent temperature fluctuations occur. If the temperature alters, the gas in the retorts will either expand or contract independently of changes in volume brought about as a result of respiration. Hence under these conditions misleading and incorrect conclusions might be drawn.

In order to *demonstrate the evolution* of carbon dioxide by living plant material the apparatus shown in Fig. 148 may also be used. Here a current of air freed from carbon dioxide is drawn slowly through a container in which the respiring material has been placed. The arrows show the direction of the flow of air. The potash in the U-tube removes the carbon dioxide from the air and so the baryta water in B remains clear. The baryta water in A soon becomes turbid, owing to the formation of insoluble barium carbonate as a result of the action on the barium hydroxide of the carbon dioxide liberated by the respiring material in the large container.

With slight modifications and the application of suitable analytical methods this apparatus can be used to determine the amount of carbon dioxide evolved, and hence to give a measure of the rate of respiration. If sugar is oxidised the volume of oxygen absorbed will equal the volume of carbon dioxide liberated according to the equation

$$C_6H_{12}O_6 + 6\ O_2 \rightarrow 6\ CO_2 + 6\ H_2O.$$

This ratio of carbon dioxide evolved to oxygen absorbed, $\frac{CO_2}{O_2}$, is known as the **respiratory quotient,** and when sugar is oxidised it approximates to unity. When other substances are being oxidised, or when the oxidation is incomplete, the value of the respiratory quotient may deviate considerably from unity. When, for instance, fats are oxidised, as in some germinating seeds, the respiratory quotient is of the order of 0·7. On the other hand in some succulents the oxidation, under certain conditions, is incomplete, and no carbon dioxide is evolved. Here the partial oxidation of the sugar results in the formation of organic acids. Sometimes, as in apple fruits, we find that organic acids are oxidised, giving a respiratory quotient greater than unity. Respiration clearly demands an abundant supply of oxygen, and respiration occurring in the presence of free oxygen is called **aërobic** respiration. Even when free oxygen is absent we find that a modified form of respiration (**anaërobic**) takes place. Most plants have the ability to respire anaërobically for short periods. Germinating peas, for instance, if deprived of a supply of oxygen, continue to liberate carbon dioxide. This anaërobic respiration results in the formation from sugar of carbon dioxide and ethyl alcohol, according to the equation

$$C_6H_{12}O_6 \rightarrow 2\ C_2H_5OH + 2\ CO_2.$$

Higher plants cannot respire anaërobically for long periods, but the process is commonly met with in the Fungi and Bacteria, some of which can only respire in the absence of free oxygen. Anaërobic respiration is a process similar to and probably identical with the fermentation of sugar which is induced by yeast.

38. Energy

The oxidative breakdown which is termed respiration results in a liberation of energy. This is so whether the substance oxidised is sugar, fat, or organic acid, and whatever the organic substances oxidised, they have been derived from the products of photosynthesis. In photosynthesis the energy of the light, which cannot be used directly in many metabolic processes, is stored as potential chemical energy within the sugar molecules. When these sugar molecules are oxidised the energy is released. As these oxidations go on in every living cell it follows that energy is released in every living cell. This is important, as the energy must be released at the point where it is to be utilised.

Some at least of this energy is used in the plant-cell to promote those syntheses that need a supply of energy. Just how the energy set free in respiration is harnessed to this purpose we do not know. A good deal of the energy liberated may be dissipated in the form of heat. This loss of heat-energy is exhibited by most actively growing organs. It is especially marked with germinating seeds, as will be seen if in each of two thermos flasks are placed dry pea seeds and soaked seeds respectively. If thermometers are inserted in the flask the temperature in the flask containing the soaked peas may be two or three or more degrees above that in the other flask.* Energy radiated as heat represents a waste of energy so far as the plant is concerned.

39. Mechanism of Respiration

It is clear that the oxidation of sugar to water and carbon dioxide in respiration is not the simple process represented by the equation

$$C_6H_{12}O_6 + 6\ O_2 \rightarrow 6\ H_2O + 6\ CO_2.$$

The first stage in the process is the hydrolysis of reserve carbohydrates such as starch or sucrose to hexose sugars. These sugars then undergo a process of activation which causes conversion of the relatively stable hexose sugar molecules into a form easily broken down. The activated sugar molecules undergo a process known as glycolysis, which is brought about by enzymes of the zymase complex. Glycolysis results in the formation of substances such as pyruvic acid and acetaldehyde. The fate of these depends on the presence or absence of oxygen. If oxygen is present they are oxidised to water and carbon dioxide. Under anaërobic conditions ethyl alcohol and carbon dioxide are produced. In the presence of oxygen all the products of glycolysis are not immediately oxidised. Some appear to be built back into the system in an anabolic process which, as it occurs only when oxygen is present, is termed oxidative anabolism. We can represent all these stages diagrammatically thus:—

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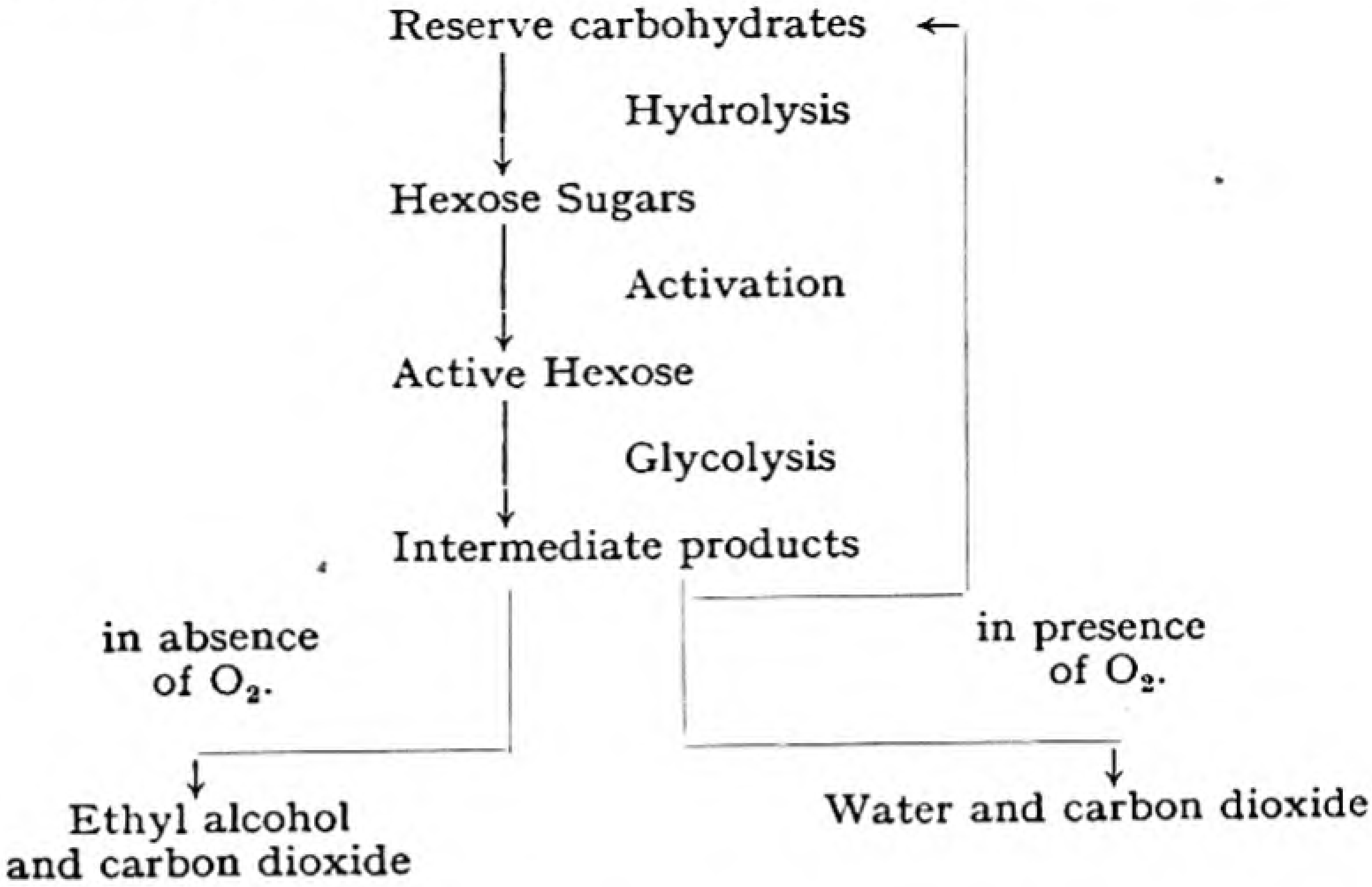
* It should be realised that, after a time, moulds may develop on the soaked peas and, if this is so, will account for at least some of the rise in temperature.


Reserve carbohydrates
Hydrolysis
Hexose Sugars
Activation
Active Hexose
Glycolysis
Intermediate products
in absence of O_2.
in presence of O_2.
Ethyl alcohol and carbon dioxide
Water and carbon dioxide

In plant tissues enzymes are known to occur which can catalyse many of the reactions involved in this scheme of respiration. We still, however, have no clear picture of how the oxidation of some of the intermediate products to carbon dioxide and water is effected. Possibly enzymes such as oxidases and peroxidases promote some of these oxidations, whilst certain pigments may act as oxygen carriers. These carriers are themselves readily oxidised by molecular oxygen, and in the oxidised state are able to oxidise other substances. These suggested reactions, however, are so far only tentative.

SPECIAL METHODS OF NUTRITION IN FLOWERING PLANTS

We have considered various aspects of the nutrition of a normal green land plant, and dealt with the methods by which such a plant obtains supplies of water, carbohydrates, proteins and minerals. Many flowering plants, however, show deviation from what we have considered as the "normal" method of nutrition. These are dealt with in the sections which follow. (Consideration of Sections 42, 43 and 44 should be deferred until Chap. XX has been studied.)

40. Parasites and Saprophytes (see p. 12)

Some flowering plants obtain their food by living as *parasites* or as *saprophytes*. Parasites and saprophytes are distinguished as *total* or *partial*, according to whether they get the whole or part only of their food in these ways. Plants which have no chlorophyll are necessarily total parasites or saprophytes, since they cannot synthesise carbohydrates from carbon dioxide, and must obtain carbon in the form of organic compounds.

41. Total Parasites

Dodder and broomrape are examples of flowering plants which, being almost or quite devoid of chlorophyll, are entirely parasitic.

The dodder (*Cuscuta*, Fig. 149, A) belongs to the Family Convolvulaceae. Common species are *C. reflexa*, *C. hyalina*, and *C. chinensis*. The seed, which contains a thread-like embryo embedded in endosperm, germinates when the plants which serve as hosts have already developed their shoots.

The seedling sends a little club-shaped root into the ground, while its shoot elongates rapidly and at the same time nutates in ever widening circles. If it meets with a suitable *host*, e.g. grasses and various herbs and shrubs, the dodder stem twines round the host plant and develops suckers or *haustoria* which penetrate into the tissues of the host. The xylem and phloem of these organs fuse with the xylem and phloem of the host (Fig. 149, B), and thus the parasite obtains supplies of organic food as well as of water and salts. Meanwhile the root of the parasite dies. The thin reddish stem branches copiously and produces small scaly leaves and numerous small clusters of flowers. If the dodder seedling does not reach a suitable host plant it soon dies.

The broomrape is a root-parasite—*i.e.* its roots are attached to, and absorb both inorganic and organic food from, the roots of other plants. It belongs to the Family *Orobanchaceae*. A common species of broomrape (*Orobanche cernua*), grows on the roots of tobacco and other crops.

Christisonia is a fleshy parasitic herb bearing scale-leaves only and found parasitising rice, bamboo and other plants. *Balanophora* is a leafless parasite, completely devoid of chlorophyll. It is attached to the root of the host, and except in the flowering season, consists only of an underground tuber. *Korthalsella* is another complete parasite, in this case parasitising especially *Rhododendron* and *Ilex*.

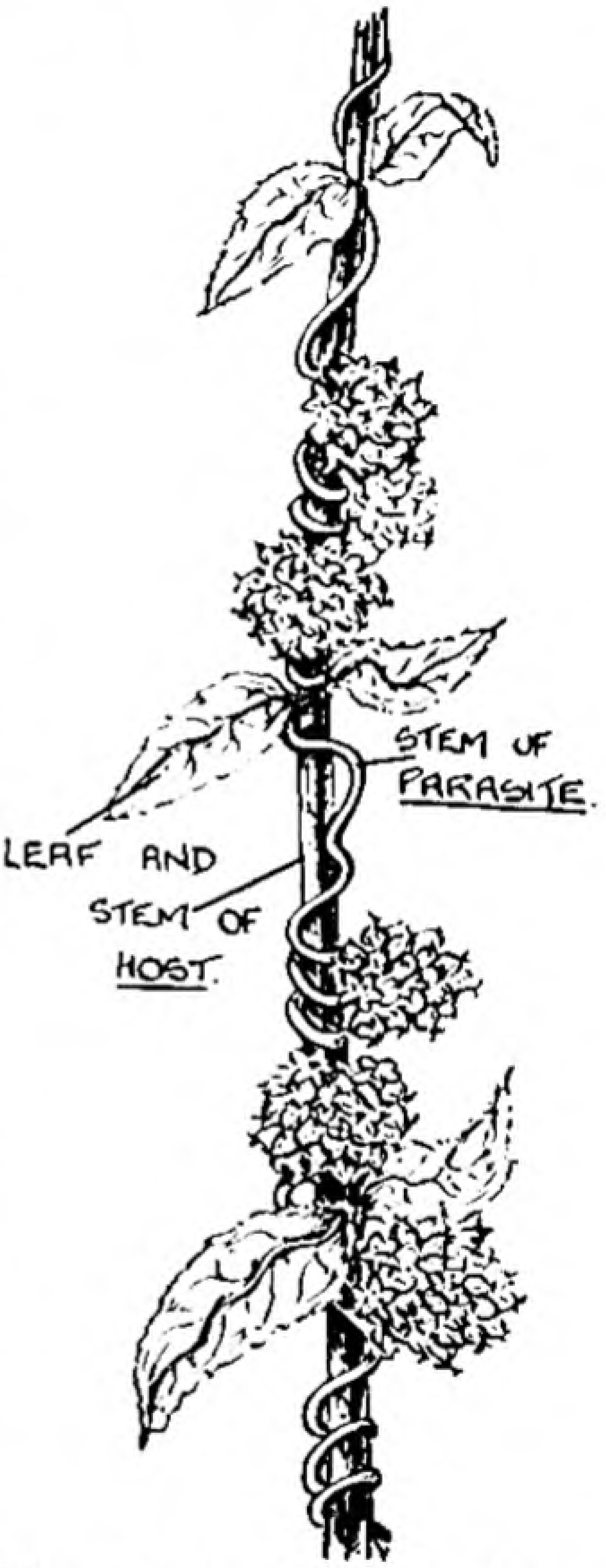

STEM OF PARASITE.
LEAF AND STEM OF HOST.

Fig. 149, A. *Cuscuta*, Parasitic on *Urtica*, External.

42. Partial Parasites

These contain chlorophyll and have normal foliage leaves, so that they can make at least part of their organic food by photosynthesis, while they draw their supply of water and dissolved salts from a host plant.

Species of *Viscum* (mistletoe) are sometimes seen in India. The seed germinates on a branch of a suitable host, and the woody tissues of the two plants become continuous (Fig. 150). *Loranthus* is represented in India by a number of species, all semi-parasitic shrubs, forming contact with the wood of their hosts. *Santalum album* is a partially parasitic evergreen shrub, the heart-wood of which yields sandal wood, from which an oil is obtained by distillation. It is cultivated in the East Indies.

Several members of the *Scrophulariaceae* are partial root-parasites. Examples are provided by some species of *Striga*. They possess chlorophyll and have ordinary roots, but where their roots come into contact with the roots of a suitable host, swellings (suckers) are formed which attach themselves to these roots from which they absorb food. *Striga lutea* is often found parasitic on the roots of *Sorghum*, where it may cause a serious diminution in the yield. Frequently the seed of *Striga* will only germinate when it is in close proximity to the roots of other plants. Presumably an exudate from these roots stimulates the *Striga* seed, so that germination occurs and the seedling then attaches itself to the root of any suitable host, if one is available. The stimulation can be provided by roots which are not themselves suitable hosts for the *Striga* seedlings.

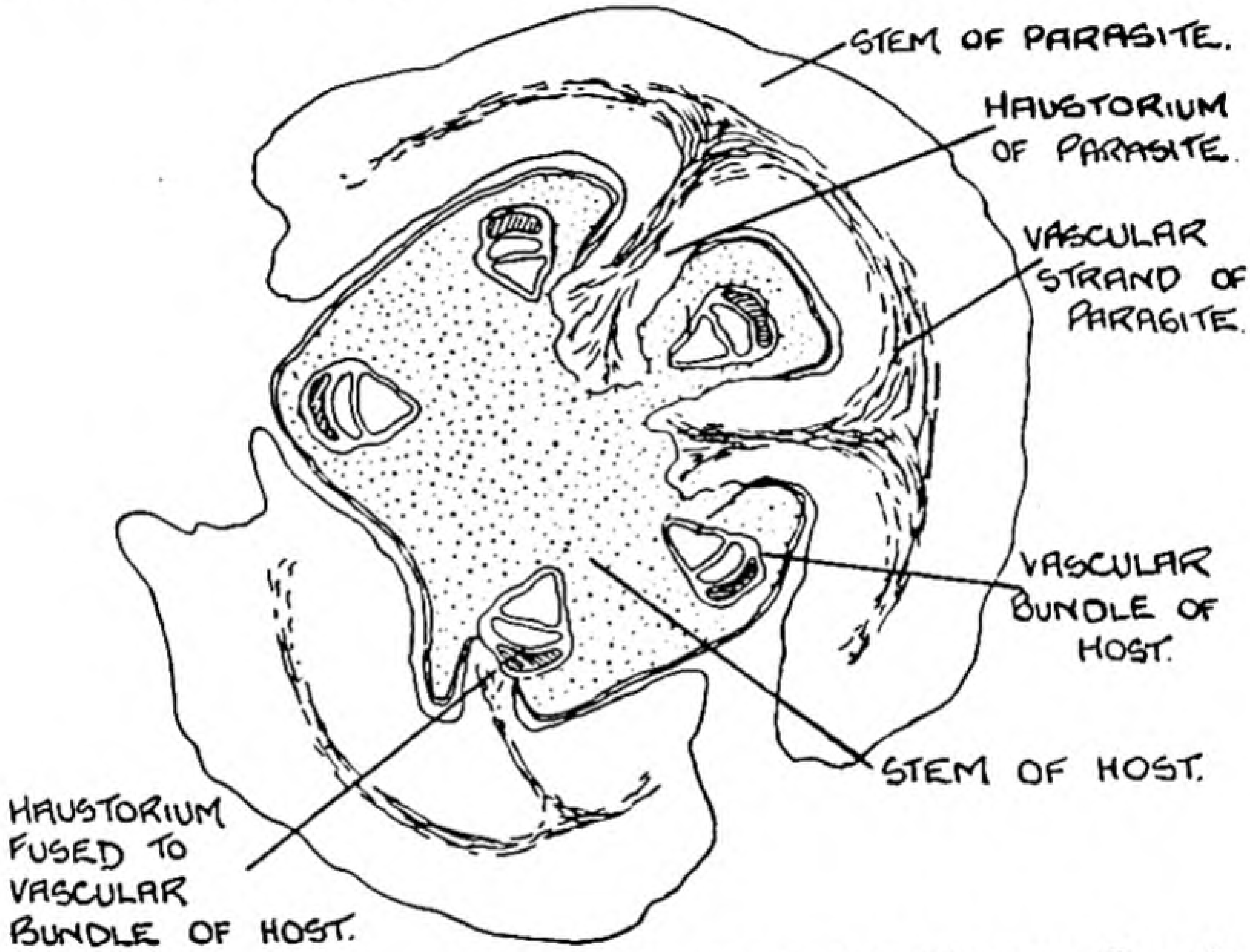


Fig. 149, B. SECTION THROUGH HAUSTORIA AND HOST OF *Cuscuta*.

43. Saprophytes

Examples of totally saprophytic flowering plants are found mainly in the Orchidaceae, e.g. *Epipogum*, *Corallorhiza*, species of *Vanilla* and the bird's-nest orchid (*Neottia*, Fig. 151, A). *Neottia* has the lower part of the stem covered with a mass of short, thick roots (hence the name " bird's-nest "), and the fleshy upper part of the stem, ending in a raceme of flowers, bears small yellowish-brown scales instead of green leaves. *Corallorhiza* has a rhizome without roots.

In these cases the plant is unable to grow in soil which contains no organic matter. It is able to make use of organic matter for nutrition by the help of a " fungus-servant." Saprophytic Fungi, by enzyme action, normally make use of the dead organic remains of plants and animals as their source of food. Whilst some fungus-threads permeate the leaf-mould, the section of *Neottia* root (Fig. 151, B) shows that others penetrate the cells of the piliferous layer and outer cortex of the root. In some of these cells the fungus-threads appear quite healthy, but in others they are in process of digestion. In the inner cortex of the root, where no fungus-threads appear, starch-grains are present. As *Neottia* is incapable of photosynthetic activity, this starch can only have come from the products of digestion of the Fungus, and indirectly from the humus in which the plant grows. The *Neottia* plant really lives parasitically on the Fungus, but the Fungus may also benefit by its association with *Neottia*. Such an intimate association of two or more organisms from which all the partners benefit is called symbiosis. In other saprophytic orchids with no chlorophyll (e.g. *Aphyllorchis montana*, *Didymoplexis pallens*, *Epipogum nutans*, etc.) the methods of nutrition are probably similar to those exhibited by *Neottia*.

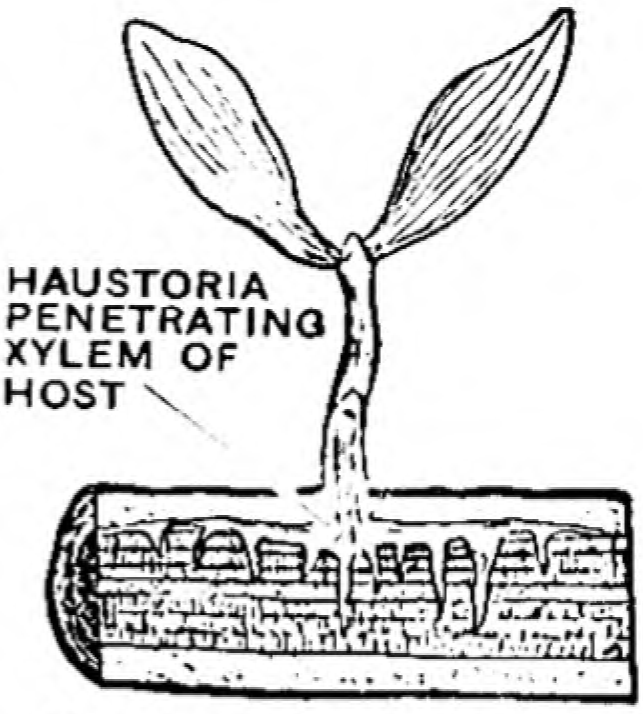


Fig. 150. YOUNG MISTLETOE PLANT, WITH TWIG OF HOST PLANT IN SECTION.

44. Mycorrhiza

This symbiotic union of a Fungus with the root of a Spermatophyte is called a mycorrhiza, and is of wide occurrence. The roots of most forest trees, and of many other plants which grow in the rich humus of woods and plantations, e.g. *Monotropa*, have an external (*ectophytic* or *ectotrophic*) mycorrhiza, while in Ericaceae (ling, heaths, bilberry, etc.), the mycorrhiza is usually internal (*endophytic* or *endotrophic*) as in *Neottia*. Most of the plants growing in the peaty soil of heaths and moors have mycorrhiza.

Roots that form mycorrhiza are usually short and stumpy and devoid of root-hairs, and the normal absorbing-functions of root-hairs are taken over by the fungal hyphae. These, because they are chemotropic and also able to absorb soluble organic substances, are probably more efficient as absorbing organs than root-hairs. The green plant appears to benefit from its association with the Fungus. What advantage, if any, the Fungus obtains from the association is not so clear.

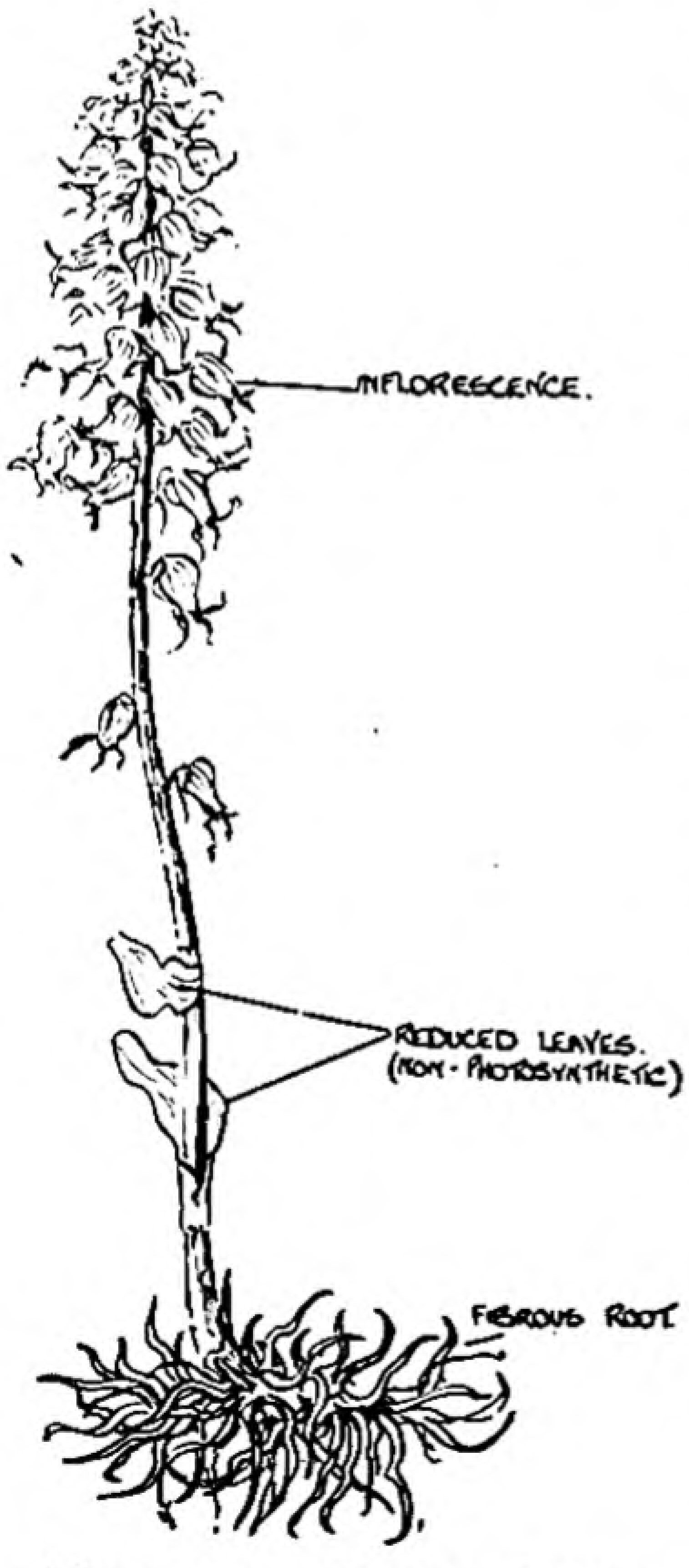


Fig. 151, A. *Neottia*, PLANT.

45. Root Nodules

In leguminous plants there is an association between the roots and a Bacterium (e.g. *Bacillus radicicola*). The Bacterium is present in the soil and penetrates the root-hairs and cortical cells of the leguminous root. The cells of the root are stimulated to divide actively so that irregular swellings or nodules appear on the root (Fig. 152, A). The central tissue of each nodule consists of cells filled with the Bacteria (Fig. 152, B). These Bacteria have the ability to fix nitrogen, *i.e.* to convert gaseous nitrogen into organic nitrogenous compounds. Some of the nitrogenous substances are passed on to and utilised by the leguminous plant, which thus has its supply of nitrogen augmented. At the same time the Bacteria obtain their carbohydrates from the host plant, and so we have an intimate association of two plants from which both members derive benefit. This appears to be a true symbiosis.

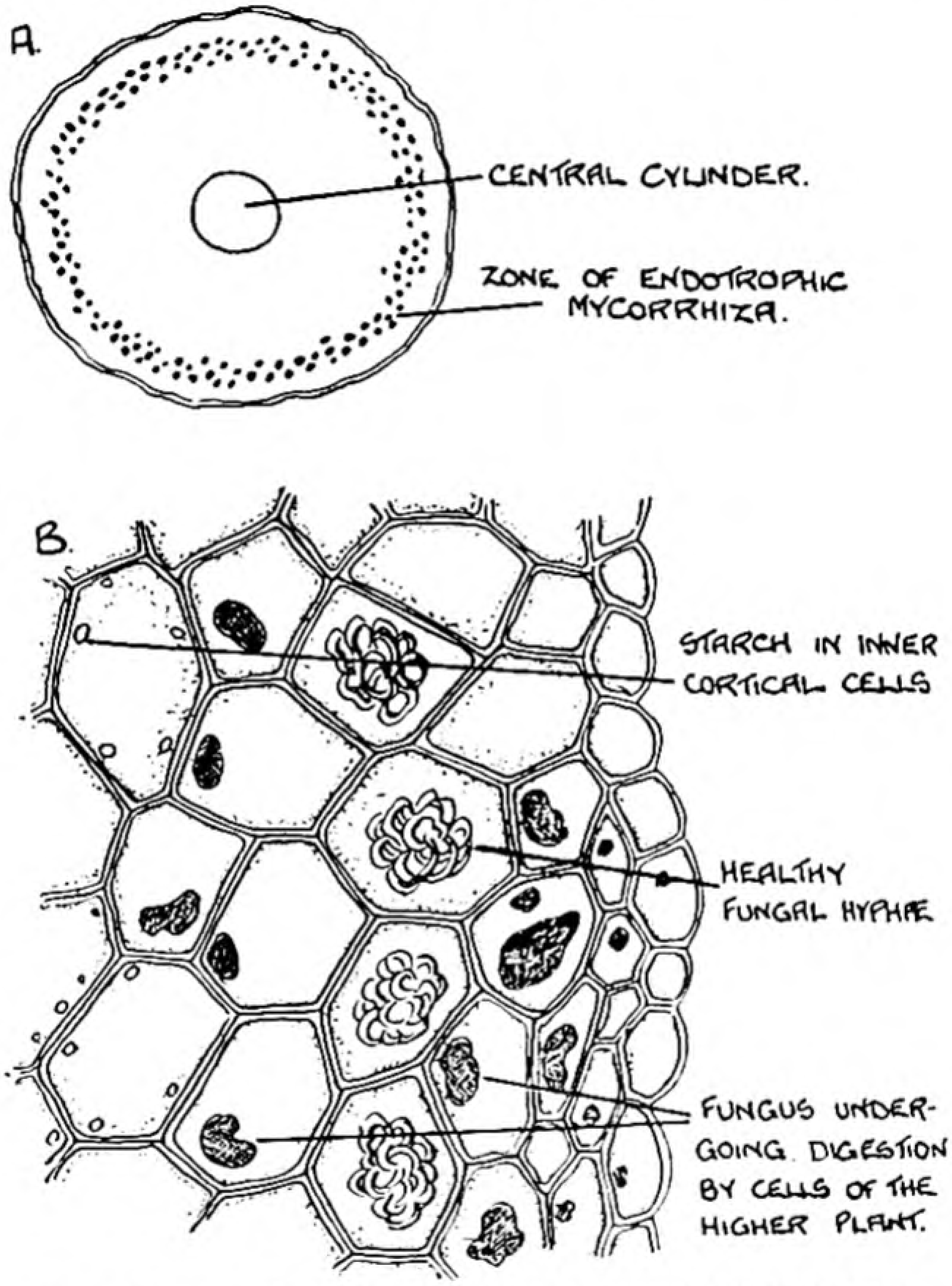

A.
CENTRAL CYLINDER.
ZONE OF ENDOTROPHIC MYCORRHIZA.
B.
STARCH IN INNER CORTICAL CELLS
HEALTHY FUNGAL HYPHAE
FUNGUS UNDERGOING DIGESTION BY CELLS OF THE HIGHER PLANT.

Fig. 151, B. *Neottia* Root, Transverse Section.
A, Diagrammatic; B, Detail of outer region.

46. Carnivorous or Insectivorous Plants

These obtain part of their nitrogenous food by catching insects in various ways, by means of modified leaves, and afterwards absorbing parts of the insect-tissue. The British insectivorous plants are the sundews, butterwort, and bladderwort.

The butterwort, *Pinguicula*, is represented in India by the Himalayan species *P. alpina*. The plant has a basal rosette of broad leaves, whose upper surfaces are covered with sticky glands, while the margins are rolled inwards slightly. Small insects are caught by the sticky secretion and washed by rain to the edge of the leaf, which curls inwards and encloses them; the glands secrete digestive enzymes, absorb the products, and the leaf becomes unrolled again.

Drosera is found in the plains, Himalaya and Nilgiris. The drops of sticky fluid, secreted by the tentacles on its leaves, glisten in the sun like dew. The tentacles stand out from the surface of the leaf like pins from a pin-cushion, and are of two kinds, longer marginal ones and shorter inner ones. Small insects are attracted and held by the secretion, and at the same time the tentacles are stimulated to movement (see p. 224). The marginal tentacles, when stimulated by direct contact, or indirectly from the shorter tentacles, bend over the insect and effectively imprison it. The stimulated tentacles also secrete a fluid which has the power of digesting, and rendering soluble, protein substances (Fig. 31). The secreted fluid is re-absorbed, together with the dissolved nitrogenous products of the insect's body. When digestion is completed, the tentacles resume their former position and are then ready to capture another insect.

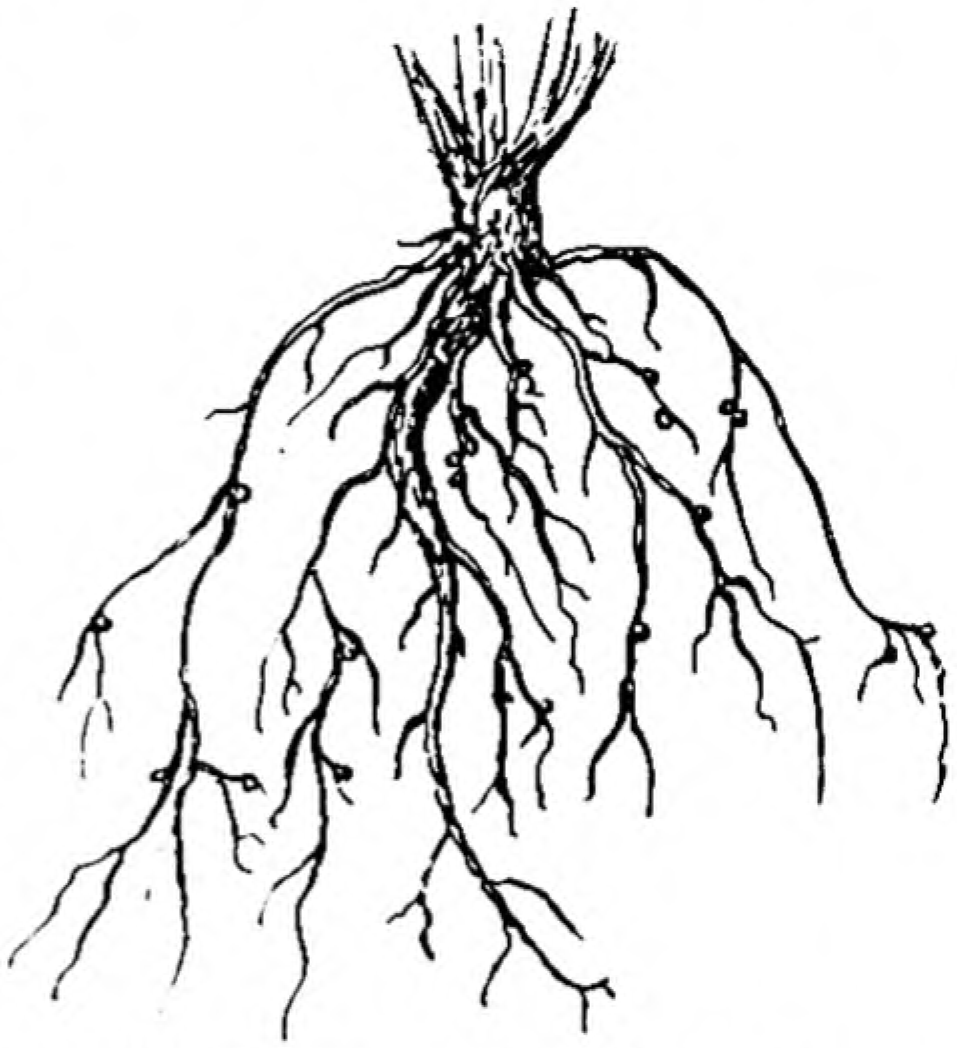


Fig. 152, A. Root Nodules.
External view of root of leguminous plant.

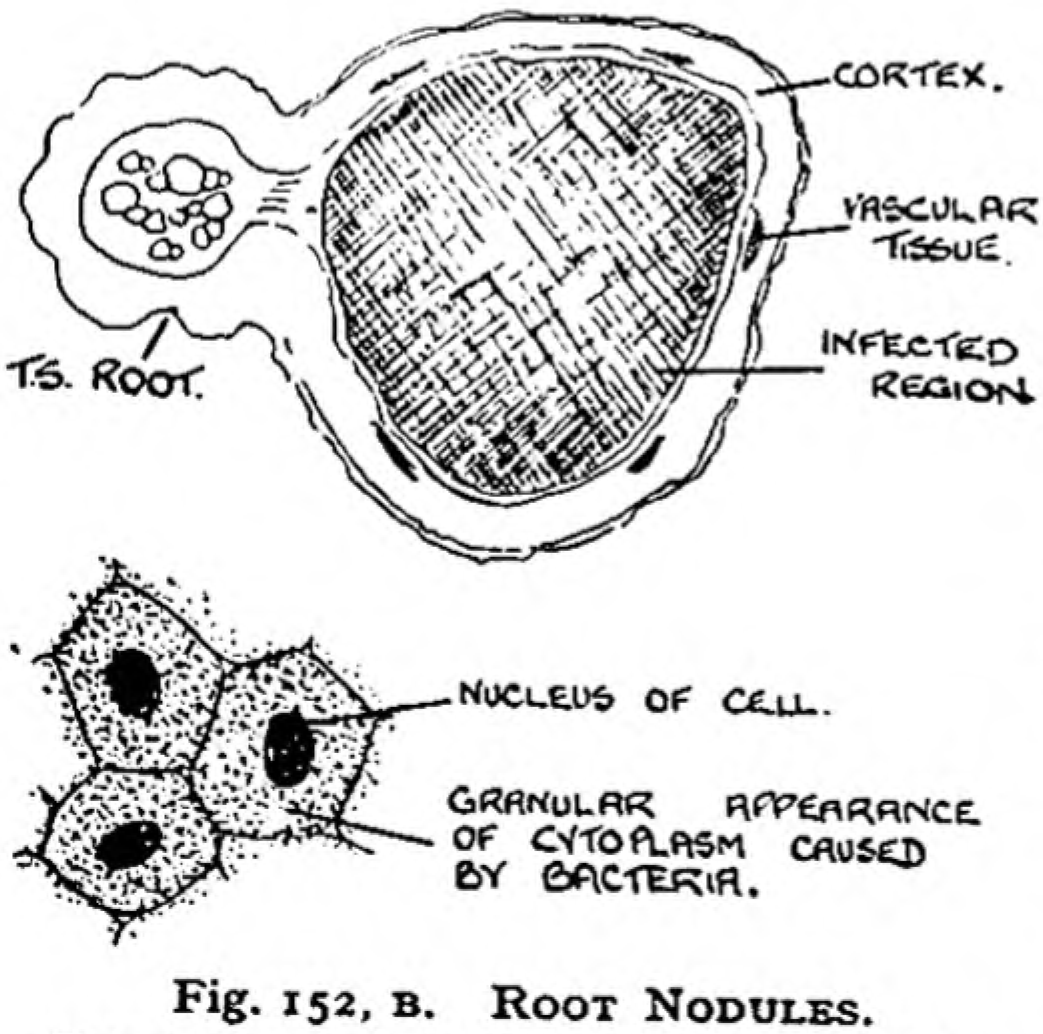


Fig. 152, B. Root Nodules.
Transverse section of root in region of nodule.

Utricularia is a genus with many species that grow submerged in water, except for the flowering shoots (*U. stellaris*, *U. flexuosa*, etc.). The plant body is not clearly differentiated into roots, stems and leaves, but, borne on the linear segments are bladder-like structures which trap small animals (insects, water-mites, water-fleas, etc.). The mechanism is extremely interesting. Each bladder is somewhat pear-shaped and attached to the plant near its broad end. The narrow end is provided with trichomes whose structure and disposition appear to guide insects to a kind of trap-door which is normally closed. Preparatory to capturing an insect the walls of the bladder are somewhat concave, and there is a negative pressure inside. Toward the middle, lower portion of the door are four stiff, curved bristles.

When the insect touches these the door suddenly opens inwards and the consequent inrush of water carries the insect inside the bladder and the door shuts. The insect cannot escape. There appears to be evidence that it is digested, but even if it merely decays the soluble parts are absorbed by the plant. The trap then resets itself by exhausting its water content. Possibly this action is assisted by characteristic trichomes, each having four terminal cells, which project into the cavity of the bladder from the inner surface. The resetting of the trap occupies about 15 to 30 minutes.

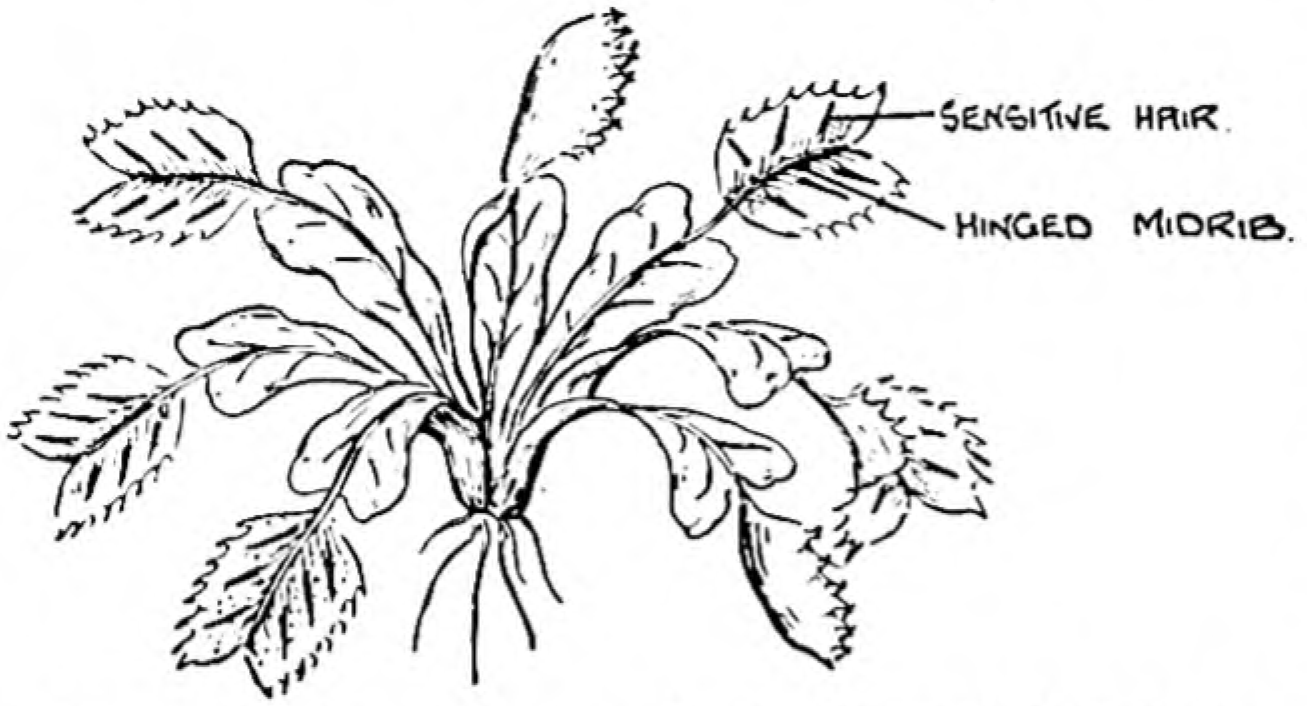


Fig. 153. *Dionaea muscipula*, VENUS' FLY-TRAP.

Venus' fly-trap (Fig. 153) is a native of Carolina, where it grows in peat-bogs; it is often cultivated in hothouses. The leaves are two-lobed, and the midrib functions as a hinge. Each lobe bears marginal teeth, and, on its upper surface three long sensitive hairs jointed at their bases. When one of these is touched by an insect, the two lobes of the leaf snap together, the marginal teeth cross one another and trap the insect. Digestive glands on the leaf surface secrete enzyme only when stimulated. The leaves of Venus' fly-trap are only slightly sensitive to chemical stimuli, but if the closing of the lobes has been caused by an insect they press tightly against each other and hold the insect fast, whereas the closing remains incomplete, leaving a wide space between the lobes, if the hairs have been touched by, say, a pencil. In the latter case the leaf opens again, but if an insect has been caught the leaf remains closed until the digested products have been absorbed.

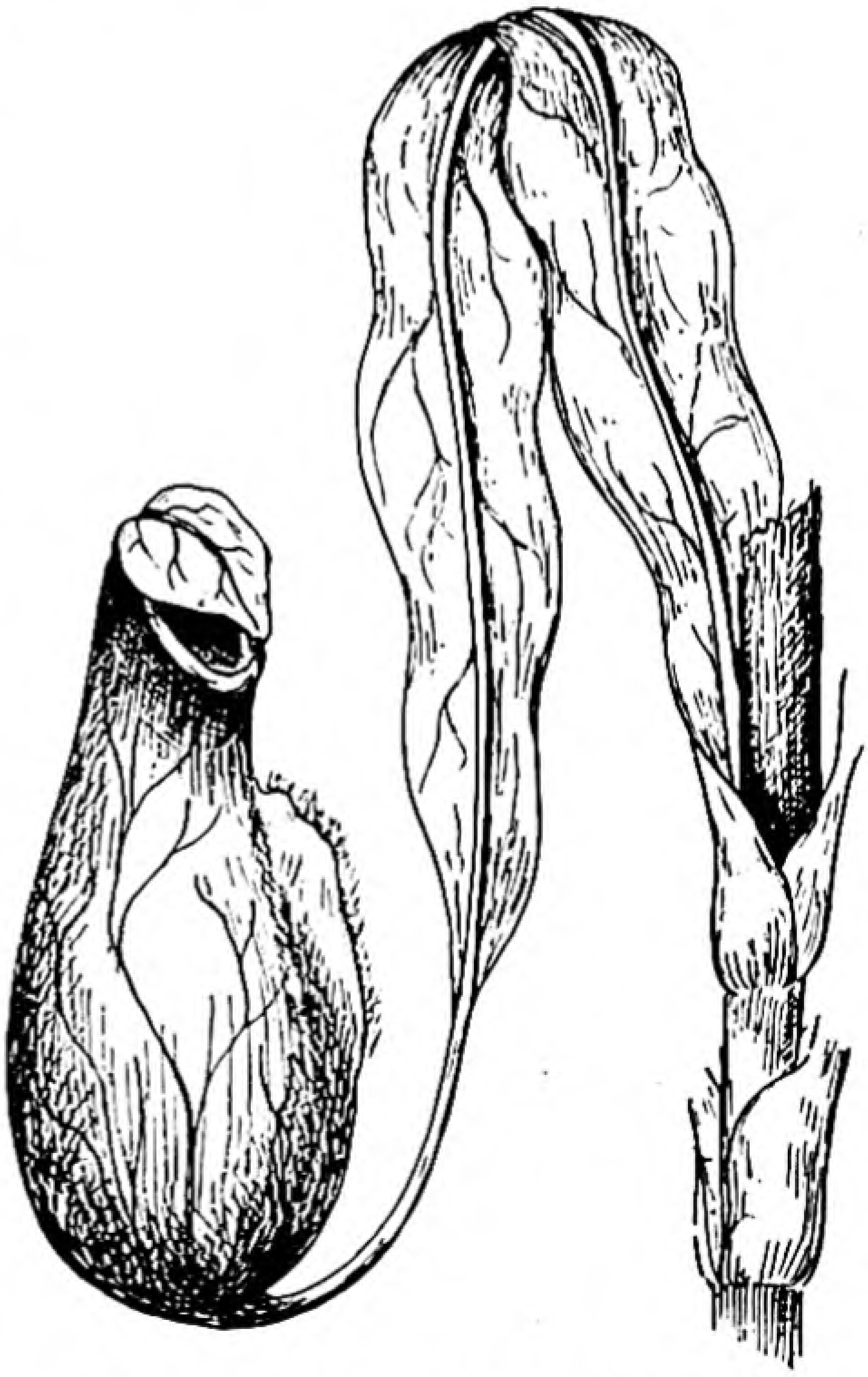


Fig. 154. PITCHER OF *Nepenthes*.

In the pitcher plants, of which *Nepenthes* (Fig. 154) is the best known example, the whole or part of the leaf is developed as a pitcher, with a lid attached to one side of the opening. The bottom of the pitcher contains water, usually swarming with Bacteria, and in *Nepenthes*, probably a digestive fluid is secreted, so that the insects falling into the liquid are first drowned and then digested.

In *Sarracenia* (Fig. 155) there is no ferment; the bodies of the insects are decomposed by the action of Bacteria, and the soluble products absorbed.

In these and other pitcher plants the lids of the pitchers are often brightly coloured and may serve to attract insects, but they have no power of movement, and cannot close when once they have opened. The rim of the pitcher also bears nectar-glands, which help in attracting insects; below the rim there comes a zone covered with small glands sunk in pits on the inner surface of the pitcher, then comes a smooth slippery region, the lower part of which has hairs pointing downwards, and finally the lowest part containing water. Insects crawling over the gland-bearing upper region soon reach the slippery zone, and are prevented by the hairs below this from crawling up again, so that they eventually fall into the liquid and are drowned.

Most insectivorous plants have enough chlorophyll to enable them to make all the organic food they need, and they can grow quite well when not supplied with insects. When fed with insects, raw meat, or boiled egg, however, the plants are more vigorous. Most insectivorous plants grow in poor swampy soil, which is usually deficient in nitrates and other available nitrogen-compounds. By the capture and digestion of insects they obtain supplies of nitrogenous food independently of the soil, and can in this way grow in localities which would otherwise be unsuitable.

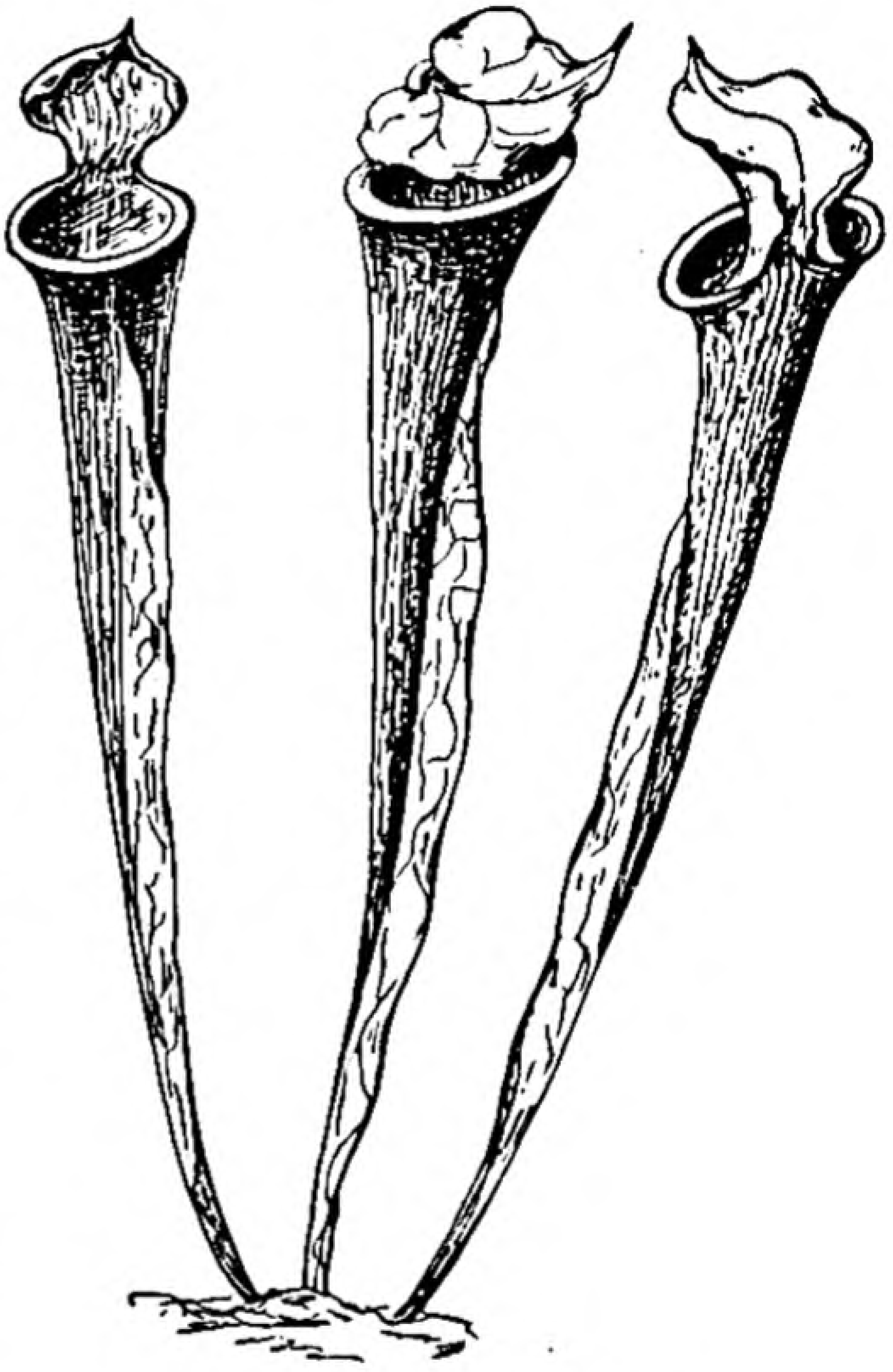


Fig. 155. *Sarracenia.*

B. GROWTH AND DEVELOPMENT

47. Growth

The capacity for growth is a feature which we look upon as a characteristic of living organisms. With unicellular plants it is true that growth of the individual consists only of an enlargement of a single cell, but with vascular land plants an increase in size is accompanied by the production of new cells and also by an increasing complexity of the plant body. All parts of the plant share in this growth and development, the activities of the different organs of the plant being correlated so that the whole plant forms a unit.

Although we are so familiar with the phenomenon of growth, both its definition and measurement present difficulties. Increase in size does not necessarily constitute growth. A flaccid cell, when it absorbs water, expands; a flaccid organ (such as a leaf), when it becomes turgid, due to the absorption of water, increases in area. This increase in area is not growth. The change in size is reversible and partial desiccation, involving a loss of turgidity, results in a shrinkage of the leaf, *i.e.* a decrease in size. Growth may most conveniently be defined as an irreversible increase in size, generally involving the synthesis of new organic substance. Usually there is also an increase in the total amount of organic substance in the plant. This is not invariably so. When, for instance, seeds germinate, or potato tubers sprout, in the dark, growth takes place. Water is absorbed, an irreversible increase in size occurs, and new tissues are produced. No photosynthesis is possible in the absence of light, but respiration goes on, so that organic matter is oxidised to water and carbon dioxide, and the dry weight of the individual decreases. There is an actual loss of organic matter. Even here there is an increase in the dry weight of the growing regions, the loss in dry weight being borne by the stored food material in the seed or tuber. With a plant able to carry on photosynthesis actively a gain in dry weight, consequent upon the accumulation of carbohydrates, is not necessarily accompanied by an increase in size, or by the production of new tissue. Therefore, although the recognition of growth is usually easy, we see that accurate definition is a matter of some difficulty. We look upon growth as the culmination of those metabolic activities of the plant that we described under "Nutrition." Substances absorbed by or synthesised in the plant are so utilised that new tissue is produced, an irreversible increase in size occurs, and we recognise that the organism has grown.

The measurement of growth is attended by several difficulties. Some of these are due to the fact that the plant is a three-dimensional object. Hence the measurement of the increase in height of a shoot, whilst it may give a useful indication of the amount and rate of growth, is not always an accurate measure. If, for instance, the height doubles and there is a proportionate expansion in other directions, the volume will have increased to eight times its original value. Similarly, if we measure shoot elongation in some trees (e.g. oak, apple), we find that it ceases quite early in the summer

(July). Increase in girth continues, due to cambial activity, and both shoot and root grow, a fact which length measurements alone fail to reveal. We have already seen with germinating seeds that the measurements of gain in dry weight do not always give a true measure of the rate or amount of growth. We conclude, therefore, that there is no one perfect way of measuring growth. The units and method of measurement have to be chosen according to the circumstances. Increase in length, area, volume and dry weight are all used as measures of growth. Sometimes it is more convenient to express growth as a proportionate rather than as an absolute increase.

48. Situation of Growing Tissues

Not all the tissues of the plant participate actively in its growth and specialised growing tissues (meristems) can be recognised. These have already been mentioned and their structure described. Growth is not confined to the meristems, but is confined to their neighbourhood. Hence it follows that only a very small proportion of the tissue of either an herbaceous or a woody vascular land plant is actively growing. The bulk of the tissues of the plant consists of permanent non-growing (and often dead) tissue.

49. Process of Growth

We have already followed the stages in growth of tissues (Chap. II, B and C). At the extreme tips of roots and shoots where synthesis of protoplasm is taking place the water supply to the cells is probably scanty. This may favour the condensation of amino acids and glucose to proteins and cellulose respectively. The substances required for the formation of new protoplasm and new cell-walls are thus available in these regions. In the growing regions we have distinguished two phases of growth, namely cell-division and cell-elongation. Where cell-elongation is taking place the growth is more rapid than where new cells are being produced. Generally, cell-division is followed at once by cell-elongation, as at the apices of roots and shoots, but occasionally the two stages are separated by a long interval of time. In the sporangiophores of *Pellia*, cell-division is completed in the autumn, but rapid cell-elongation takes place some months later in the following spring, and as a result of this extension (growth) of the cells already present, the length of the sporangiophore in the course of a few days increases to forty times its original value.

50. Regions of Maximum Elongation

If the root of a germinating seed is marked in millimetre lengths from the tip and left to grow for a short period (about three hours), it will be found on remeasuring that the zone about six or seven millimetres behind the tip has elongated most. This is where rapid cell extension is taking place. On either side there is a gradation to a slight increase in length at the tip, and to no increase in the region from about fifteen millimetres from the tip backwards. As time passes, the rate of growth of a millimetre zone near the root-tip will wax and wane, and the zone of maximum elongation will always be in the same position relative to the root-tip, which, all the time, is being pushed forward by the growth behind it.

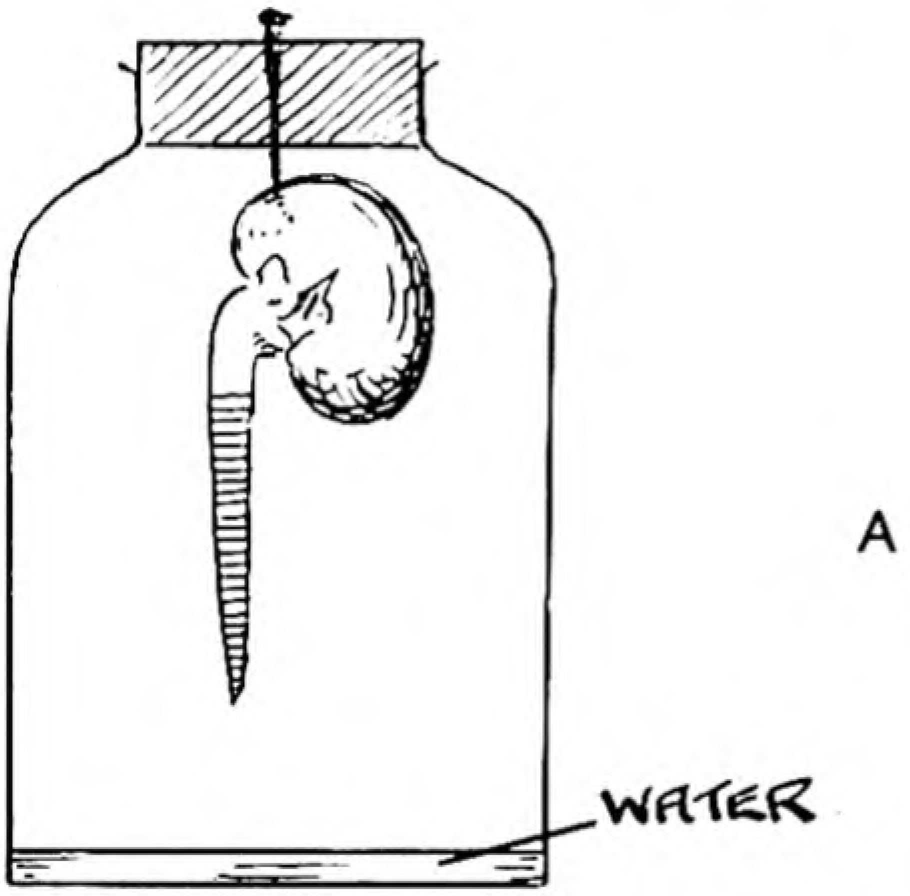


Fig. 156, A. Apparatus to show region of Maximum Growth in a Root.

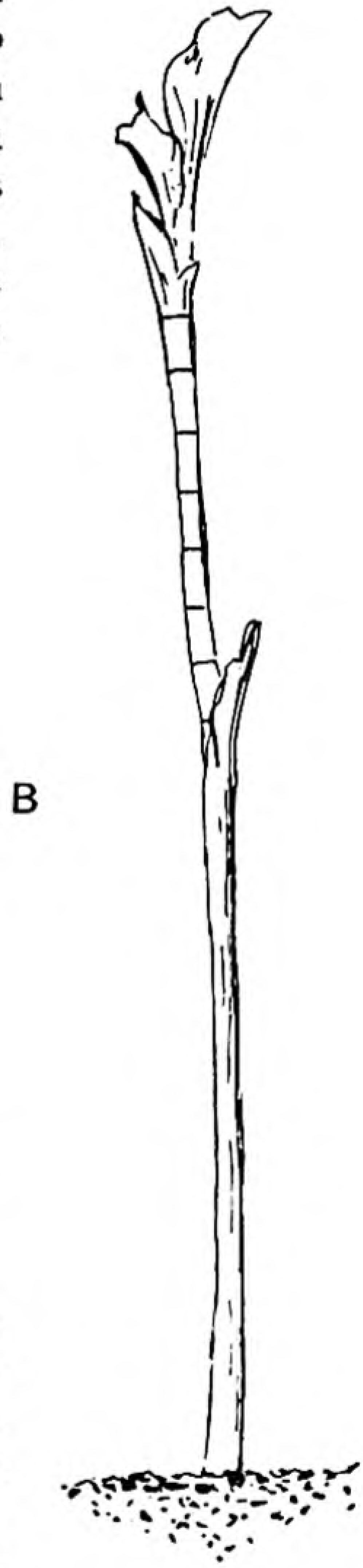


Fig. 156, B. Shoot marked off in 4 mm. Zones. to show region of Maximum Elongation.

Observations which illustrate these points may be made on a seedling of pea (*Pisum sativum*) or broad bean (*Vicia faba*), using the apparatus depicted in Fig. 156, A. The localisation of the region of rapid elongation just behind the root-tip is noteworthy as, by its means, the root-tip is forced through the soil. In the stem, on the other hand, the region of active growth is much longer than in the root, up to two centimetres or even more (Fig. 156, B). Further, the stem is divided into definite segments, the internodes, each of which grows more or less independently of the rest. Leaf growth is more complicated. Unlike the stem the leaf is usually an organ of limited growth, and its growth consists mainly of increase in area. In the broad flat leaves of most dicotyledons meristematic activity almost ceases at a very early stage in the development of the leaf. Further growth is by cell enlargement and differentiation. Many monocotyledonous leaves have a basal (intercalary) meristem which may continue to function for a long time. In such leaves new tissue is still being produced at the base when the apical part of the leaf is mature, or may even be withering.

51. Changes in the Rate of Growth

We have already seen that when a meristematic cell has divided the two daughter cells expand. At first this cell-expansion is a slow process, *i.e.* growth is slow. If one of the daughter cells is destined to form a unit cell of a permanent tissue this period of slow expansion is followed by vacuolation and rapid cell-extension, *i.e.* growth is rapid. Then, the rate of vacuolation and cell-extension gradually slows down and finally comes to a stop. Growth of a single cell, then, is at first slow, then rapid, then slow again, and finally ceases. The same is true, as has been shown, for a millimetre zone marked at the root-tip. Again, if we follow the growth of an organ, e.g. root, internode, whole shoot or leaf over a sufficiently long period (days or weeks) we find similar changes in the rate of growth. This is shown graphically in Fig. 157. Here the length of the coleoptile of an *Avena* (oat) seedling has been plotted against time. We see that at first elongation is slow, then there is a period of rapid extension, followed by a slowing down and finally by

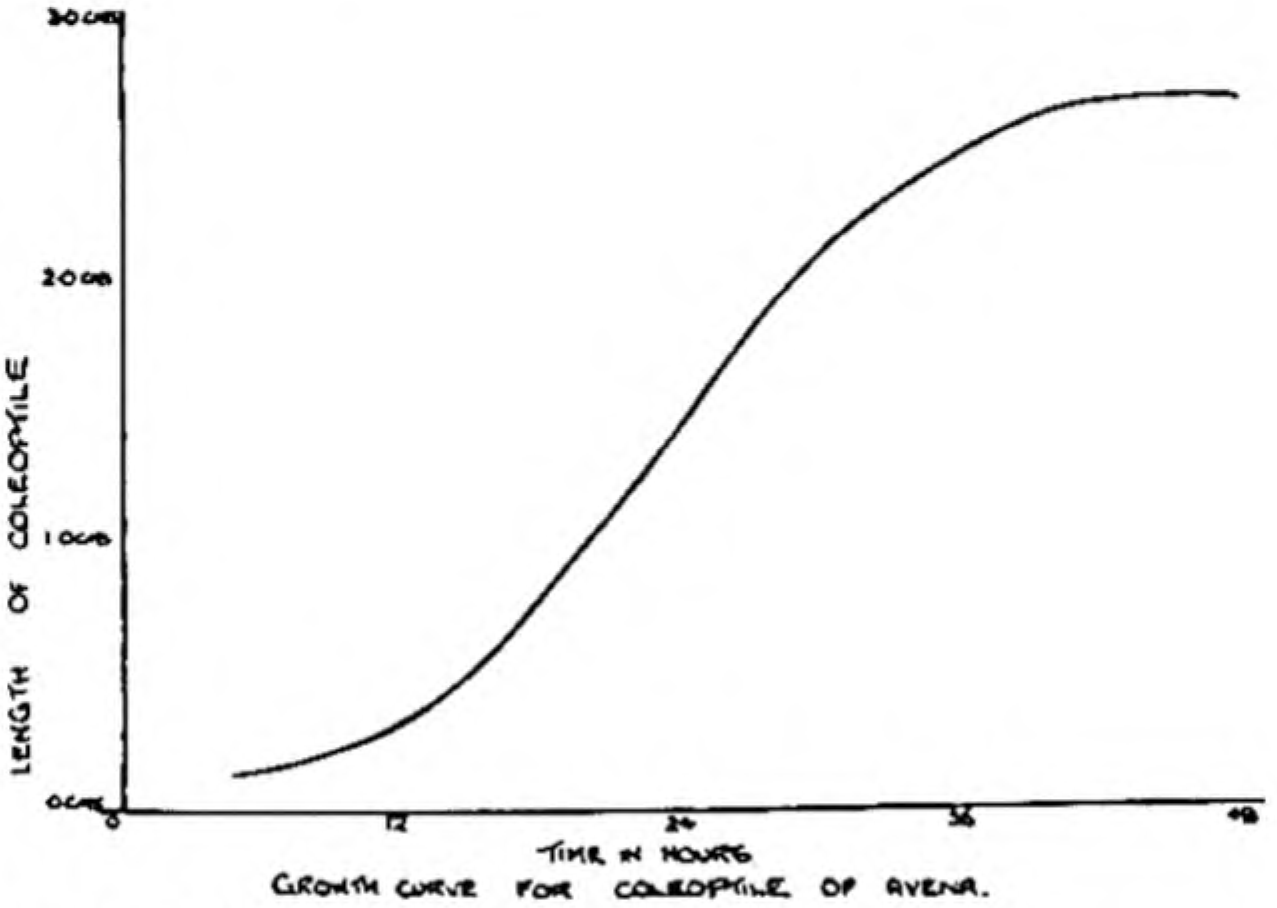


Fig. 157. LENGTH OF THE COLEOPTILE OF *Avena* PLOTTED AGAINST TIME.

a cessation of elongation. The growth of a whole plant may follow an essentially similar course and the three phases of growth, *i.e.* slow, rapid, slow, constitute the **grand period of growth.** A single cell or organ passes through this cycle of changes only once. In perennials the cycle is repeated each year during the growing season.

The reasons underlying these changes in growth-rate are not clearly understood. As the plant grows an increasing proportion of its cells become transformed into permanent tissue no longer capable of growth. A high growth-rate cannot be maintained in the absence of an abundant supply of water and food materials, and in some plants a fall in the growth-rate coincides with the diversion of large amounts of food-materials to the reproductive organs.

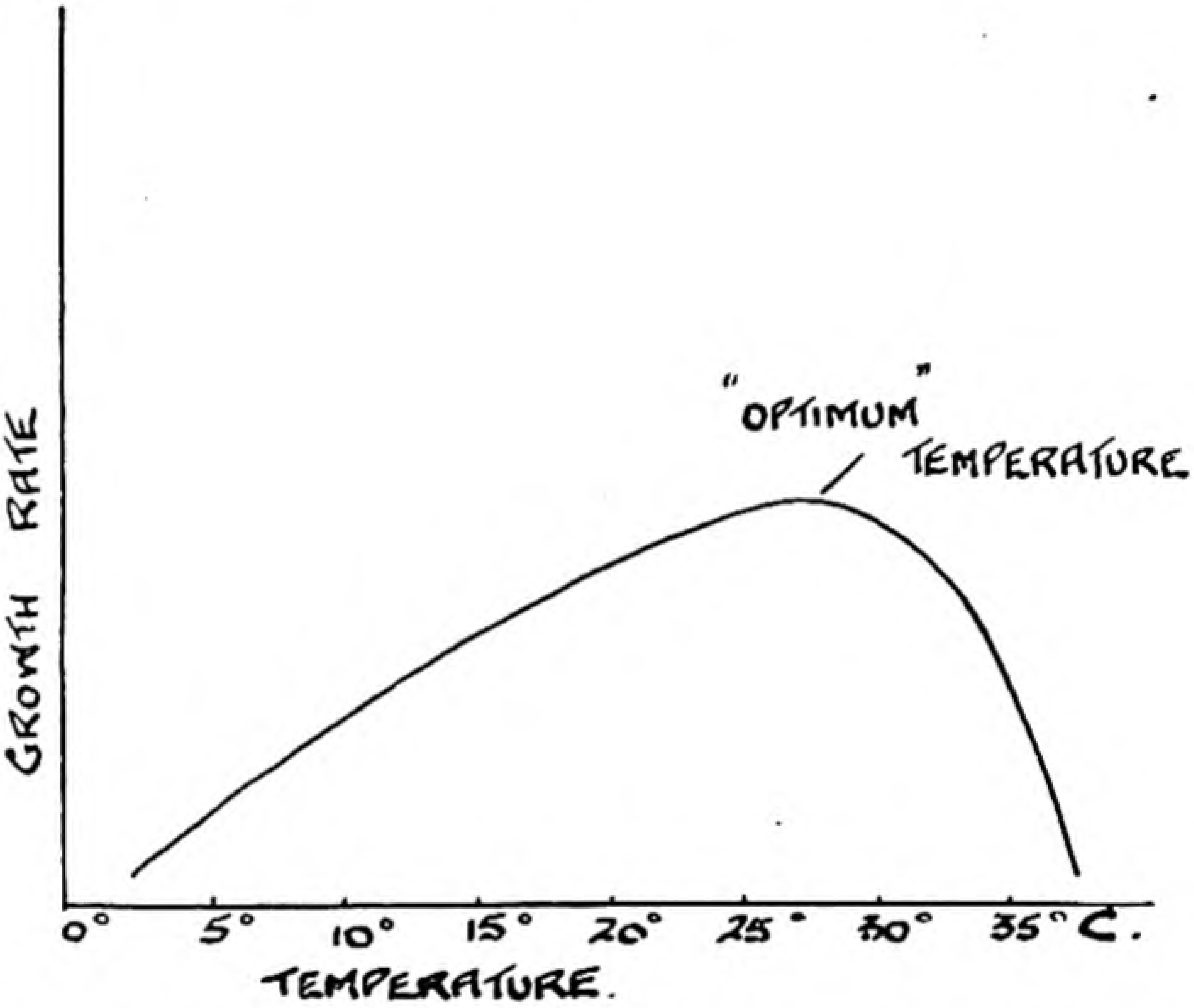


Fig. 158. GRAPH TO SHOW RELATION BETWEEN GROWTH-RATE AND TEMPERATURE.

The growth of colonies of unicellular plants, or of small plants where there is no extensive differentiation of tissue is somewhat simpler and capable of a more detailed analysis. In colonies of yeast (p. 489) and of duckweed (*Lemna*) rate of growth can be measured by determining the increase in the number of individuals. With these simpler organisms unrestricted growth can continue certainly for a long time and possibly even indefinitely when no shortage of food or oxygen develops, and when any toxic products of metabolism are removed.

52. Factors Affecting Rate of Growth

We have seen that in the grand period of growth of a single cell, an organ or a whole plant growth may be slow at first, then rapid, then slow again, and finally it ceases. These changes appear to be partly an expression of functions inherent in the plant, but they can be modified by external conditions such as alterations in nutrient supply.

Growth represents the culmination of the metabolic processes of the plant, and, as with all the vital processes, is affected by temperature. If the relation between growth-rate and temperature is shown graphically as in Fig. 158, we see that we have the well-known " optimum " type of curve. Just as with respiration, photosynthesis and other physiological processes, there are two extremes of temperature, a minimum and a maximum, below and above which no growth takes place. Between these there is the so-called optimum. The primary relation between temperature and growth, which is probably represented by Fig. 158 only over a limited temperature range, is, that for each rise in temperature of 10° C. the growth-rate is roughly doubled. At higher temperatures the primary accelerating effect is masked by a secondary harmful effect. The extent of this secondary effect depends on the period of exposure to the elevated temperature. Temperature increase, then, accelerates growth to much the same extent as it accelerates the rate of a chemical reaction. This provides evidence that growth is itself controlled by some chemical reaction sensitive to temperature changes.

The relation of light to growth is very complex and depends partly on the intensity of the light. Complete darkness, as we have seen (p. 78), results in etiolation, and in etiolated plants there is, among other changes, accelerated elongation of the internodes. In addition to any direct effect of light on growth, there is a secondary effect, as it may govern the supply of food materials. The supply of organic materials necessary for the building up of new tissues depends ultimately on the photosynthetic activity of the chlorophyll-containing tissues of the plant. Darkness may interfere with the supply of carbohydrates especially. Even if there is some internal store of carbohydrates, the onset of dark-induced starvation is only postponed. The direct effect of both temperature and light on growth are generally immediate.

Changes in the supply of water and mineral-salts more usually have a delayed effect, sometimes in addition to an immediate one. A shortage of water restricts the growth of the seedling of an annual plant. This retarding effect of the water shortage remains evident even if, at a later date, the water supply becomes adequate.

With land plants water shortage, by bringing about stomatal closure, reduces the diffusion of carbon dioxide into the leaf, and hence may reduce growth by inducing an internal shortage of carbohydrates. By its effect on growth the water supply greatly influences the yield of economic crop plants and may be a decisive factor in determining the manner of utilisation of large tracts of land. Growth, too, is reduced if the supply of any of the essential nutrient salts is restricted. The effect of salt supply is complex, partly because each essential element fulfils a number of functions in the plant. Further, the response of the growth-rate to alterations in the supply of one element, e.g. nitrogen, is conditioned by the level of the supply of other nutrients and of water. If more than one nutrient is in short supply, increases in the amount of one may be without effect on the growth, unless the others are increased also.

When the supplies of water and all other nutrients are adequate, the temperature is suitable and aërobic respiration is proceeding normally, growth generally occurs. Growth does not result automatically from a sufficiency of food materials. It is evident only in the presence of accessory growth factors. Much of the work leading to an understanding of the part played by these accessory factors on growth has been conducted on the coleoptile of *Avena*. These accessory factors, usually called growth substances or **auxins**, are in fact hormones. Hormones, secreted mainly by the ductless glands in higher animals, and markedly affecting their activities, have long been known. The evidence for the occurrence in plants of hormones has only recently become convincing, although the existence of such substances has long been suspected. The auxins or plant-growth hormones may be looked upon as chemical messengers affecting parts of the plant other than those in which they are produced.

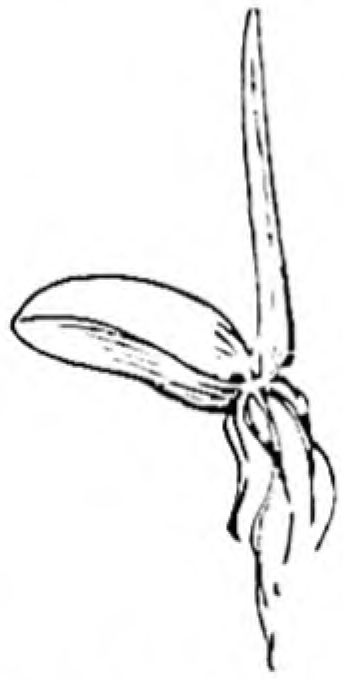


Fig. 159. OAT SEEDLING, NORMAL COLEOPTILE.

In the coleoptile of *Avena* (Fig. 159) cell-divisions cease at an early stage in growth, and the later stages of growth consist entirely of cell-elongation. In the dark the elongation is such that the coleoptile may attain a length of 6 cm., three times longer than when illuminated. If the tip of a growing coleoptile is removed, the growth of the stump is much less than that of a normal coleoptile. If the cut-off tip is replaced on the stump growth is resumed, and nearly reaches its former level. On the reheaded stump, the tip is still separated from the stump by a thin aqueous layer. There is no protoplasmic connexion between tip and stump. The resumption of growth in the reheaded stump is due to the ability of the auxin in the tip to diffuse across the aqueous separating layer into the stump, and the presence of auxin permits growth to take place. Auxin itself controls the process of cell extension. In the intact coleoptile auxin synthesised at the tip diffuses downwards, and in so doing promotes cell-elongation provided that water and food supplies are adequate. Whether in this process the auxin is itself used up is not clear. This phenomenon appears to be general. Auxin is synthesised in stem apices and young leaves, and in its downward diffusion through the stem it promotes that phase of growth represented by cell extension. Within limits the amount of cell-extension is proportional to the concentration of the auxin. In roots the effect of auxin is different. The same concentration of auxin that accelerates stem growth retards root elongation. Two auxins, auxin *a* and auxin *b*, are known to occur in green plants. A third substance, β-indolyl acetic acid or heteroauxin, is synthesised by many Fungi, and appears to have the same effect as the true auxins on growth. Many other chemical substances have been synthesised which possess some of the properties of the auxins. It is interesting to note that the auxins are not specific. The auxins from a wide range of plants appear to be identical.

53. Correlation

When a plant grows it does so as a unit. The different organs and parts of the plant do not grow independently. Each affects the others, and this influence that the cells of the plant exert on each other we speak of as **correlation.** As a result of this we can say that the plant maintains its balance. A proper ratio of root growth to shoot growth, and of stem growth to leaf growth is maintained. An increase in the transpiring leaf surface is accompanied by an apparently automatic increase in the amounts of the absorbing and conducting tissues.

The importance of the correlating influences is perhaps best realised when the results obtained by upsetting the correlation are observed. A broad bean plant, for instance, generally grows into a single unbranched stem. Buds present in the axils of the leaves remain dormant. If the terminal bud of the main shoot, or even all the young leaves near the stem apex are removed, some of the axillary buds grow out into lateral shoots. Evidently the young leaves near the stem apex were inhibiting the development of the axillary buds. The inhibiting effect appears to be due to a hormone, possibly identical with auxin, which is synthesised in the young leaves, and in its downward passage through the stem inhibits the development of the axillary buds. The leaves exert further correlating effects, also probably hormonal in nature. The young leaves certainly synthesise auxin, which passes down the stem and in so doing promotes cell (and hence stem) elongation, and the auxin, or another hormone, induces the cambium cells to divide. Hence as the young leaves expand, new and extra conducting tissue, derived from the cambium, is produced, so that a full supply of water to the increased transpiring surface can be maintained. Root production, too, may be dependent on hormone control. Certainly the production of adventitious roots on detached shoots (cuttings) of many plants is stimulated by auxins, and root production in the intact plant may be controlled in somewhat the same way. Another hormone, too—Thiamin or Vitamin B_1—may be concerned in root production and growth. This we know is present in some green plant tissues and may be translocated down to the region where root growth is to occur. Vitamin B_1, too, is present in some seeds and may exert an influence on the growth of the embryo in the seed. As a result (either direct or indirect) of the hormonal and other mechanisms, the proper amounts of food materials are diverted to root growth, shoot growth, leaf growth, etc., and normal growth of the plant as a whole ensues.

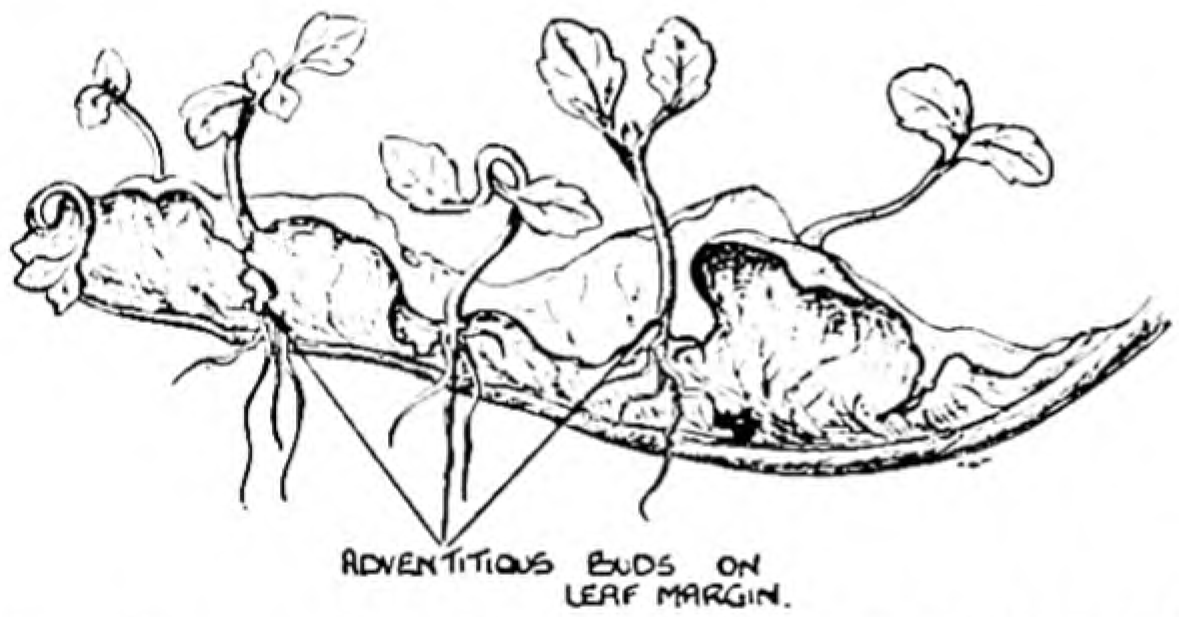

ADVENTITIOUS BUDS ON LEAF MARGIN.

Fig. 160, A. *Bryophyllum pinnatum* LEAF WITH ADVENTITIOUS BUDS.

It is well to realise that all the living cells of the plant carry all the genes, and therefore all the inherited characters (p. 539) of the plant. Every living cell of the plant, therefore, carries exactly the same propensities for growth and development that were possessed by the zygote. These unsuspected possibilities are sometimes realised in tissues removed from the correlating influence of the rest of the plant. They find expression in the ready production of adventitious roots by cuttings, in the production of both adventitious roots and buds by the cells of leaves on the plant (e.g. *Bryophyllum*, Fig. 160, A) or detached and cut across (e.g. *Begonia*), and in the formation of adventitious buds on detached pieces of root of seakale (*Crambe maritima*, Fig. 160, B), dandelion (*Taraxacum officinale*) and *Anemone japonica*, etc.

54. Development

Growth of a land plant is generally accompanied by an increasing complexity of the plant body. Characteristic changes in the form of the plant may occur and finally a phase of reproductive activity sets in. Whereas growth implies increase in size, development denotes increasing complexity and specialisation of the constituent organs of the plant and the passage from seed to seedling, from seedling to adult vegetative phase, and the onset of reproduction.

The processes involved in the germination of seeds have already been described. It is important to realise that in the seed there is an embryo or young plant which has been in existence for some considerable time. Associated with the embryo is a store of food. In a dry seed the embryo is relatively inactive—it is said to be dormant, and germination involves the resumption of intense metabolic activity. Seed formation, then, is generally followed by a period of dormancy, which in turn is followed by germination. This dormant period is, in many seeds, a necessary prelude to germination. The seeds of most willows germinate soon after they are shed from the plant. The resting period here is very short. In some tropical plants (e.g. *Rhizophora*, a mangrove) there is no

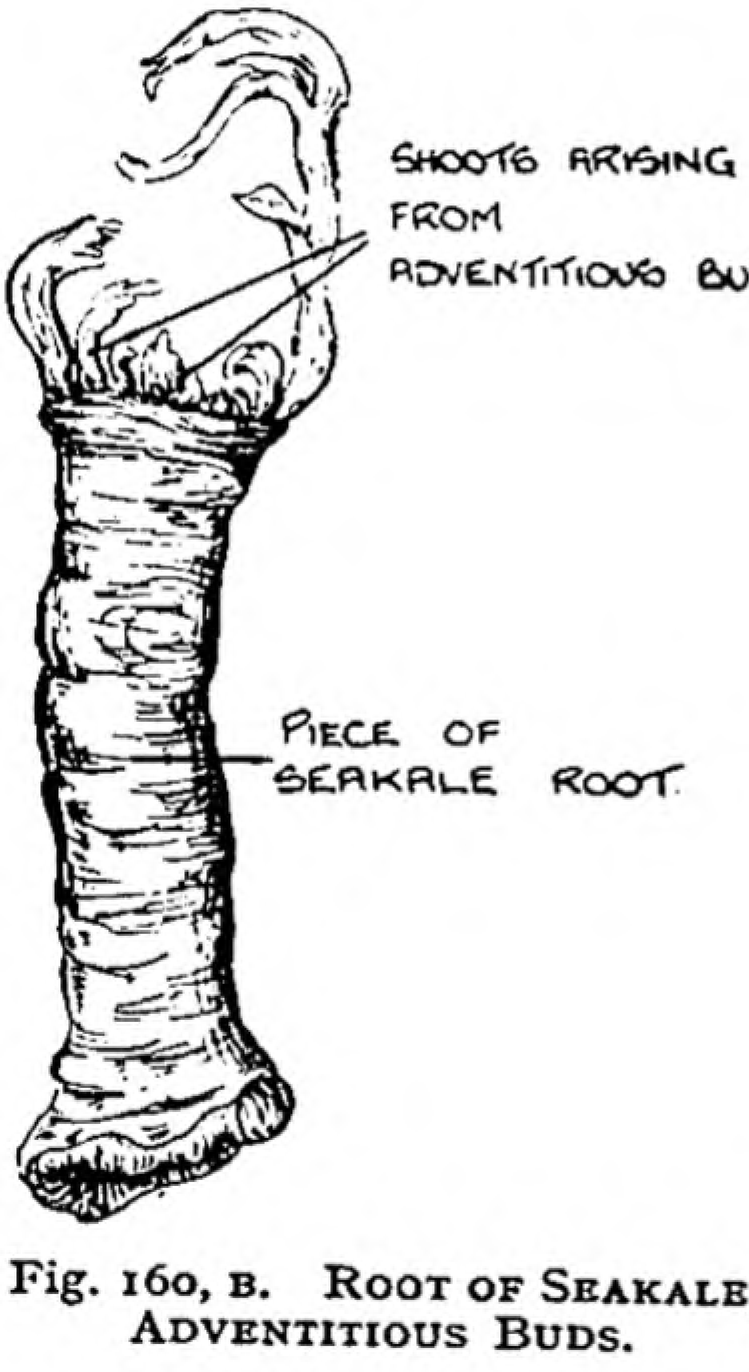

SHOOTS ARISING FROM ADVENTITIOUS BUDS
PIECE OF SEAKALE ROOT

Fig. 160, B. ROOT OF SEAKALE, ADVENTITIOUS BUDS.

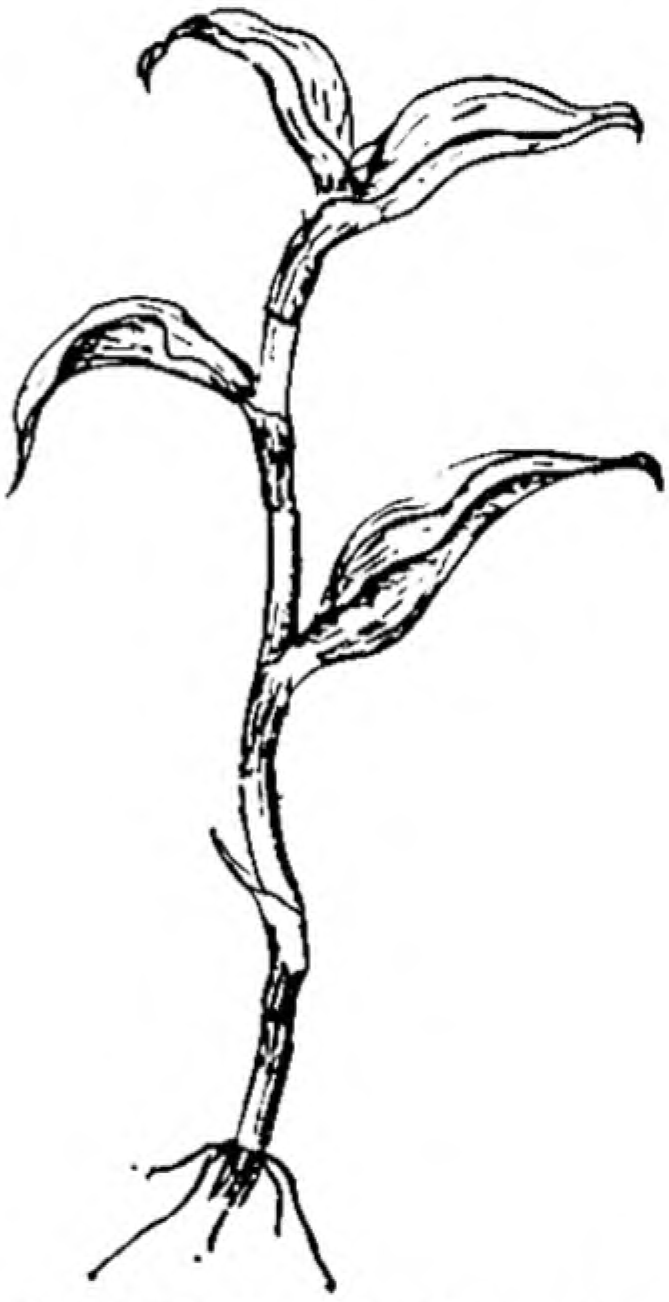


Fig. 160, C. *Tradescantia* CUTTING WITH ADVENTITIOUS ROOTS.

resting period, and the seeds begin to germinate whilst still on the tree (so called viviparous germination). These cases, however, are somewhat exceptional. More usually we find that if seeds are sown immediately after they are shed from the plant they do not germinate, even although the external conditions appear to be favourable.

The delayed germination may be due to a variety of causes. In some, the seed coat is hard and impermeable to water. We see this in the seeds of the broom, gorse, and some varieties of sweet pea. Here water absorption, and hence germination, does not occur until there has been some injury to the seed coat. In *Ranunculus ficaria* the embryo is immature when the seed is shed, and goes on growing in the seed for several months. Only after this period of development can germination occur. In *Juniperus* and *Crataegus*, although the embryo is apparently fully developed when the seed is shed, it requires a period of "after ripening" before it can germinate. When in the dry, dormant state some seeds can retain their vitality for a considerable time. Wheat may retain its vitality for fifteen years, but the most striking example of longevity of seeds is furnished by *Cassia bicapsularis*, seeds of which have germinated after a period of eighty-seven years in a dry condition. Reports of seeds of great antiquity removed from Egyptian tombs and showing ability to germinate can be discounted. Not only do dry seeds retain their vitality for considerable periods, but seeds may persist in a moist state in the soil for many years and retain the ability to germinate. There is evidence that the seeds of many common weeds (*Capsella bursa-pastoris*, *Brassica arvensis*, etc.) may lie dormant in the soil in this way for sixty years or possibly longer.

When germination does occur, there is usually a rapid acceleration of the metabolic processes and a seedling develops. The seedling is not simply a miniature adult plant. It sometimes differs in form from the adult. The seedling gorse, for instance (Fig. 112, c), possesses small flat trifoliate leaves, whereas in the adult plant the leaves are represented by spines. The seedling soon passes into the adult form and growth continues, but sooner or later the period of vegetative activity is interrupted either by the onset of a reproductive phase or by a dormant period. The assumption of dormancy is well exemplified in many perennial plants, especially in regions with a climate having well-marked seasons. In Great Britain marked vegetative activity occurs during the spring and summer. The cold winter is a period of rest. Many bulbous plants, in their natural habitat, grow actively during the wet and comparatively warm winter and rest through the hot, dry summer. The alternation of periods of activity and rest is sometimes imposed on the plant by external conditions. Thus the shoots of many willows and roses grow in length throughout the summer and cease growth when the temperature falls in the autumn. If they are protected from the autumnal fall in temperature by growing them in a greenhouse, normal growth continues throughout the autumn and winter. The periodicity in growth that they usually exhibit is imposed on them by external conditions. On the other hand the lilac (*Syringa vulgaris*) and the beech (*Fagus sylvatica*) cease growth in the late summer or autumn, and enter on a period of rest even if external conditions are favourable to growth. The periodicity here appears to be the expression of an inherent character of the tree. If many trees of temperate regions are grown in the tropics where conditions remain favourable for growth throughout the year they may continue to exhibit a periodicity of growth, but the annual rhythm tends to be lost.

Normally, after a certain period of growth, reproduction occurs. In temperate regions annual plants usually produce their seed at the end of a summer of vegetative growth. Many perennials, on the other hand, flower early in the spring before their leaves unfold. The causes underlying these differences are not understood, and we have only a very incomplete knowledge of the reasons for the onset of reproduction. Frequently reproduction appears to be favoured by an accumulation in the plant of carbohydrates and a slight internal deficiency of nitrogenous material; that is, by a high carbohydrate/nitrogen ratio. It is not clear, however, whether flowering is caused or only accompanied by this high carbohydrate/nitrogen ratio. Certainly abundant supplies of nitrate, which on absorption reduce the carbohydrate/nitrogen ratio, do quite often delay flower production. Clearly illumination will be important, owing to its effect on photosynthesis, and hence on carbohydrate supply. Light has other effects also, and in some plants the initiation of flowers is conditioned by the length of the daily periods of illumination. If the daily illumination is artificially increased many plants come into flower at a much earlier date than usual. Examples of such long-day plants are *Raphanus Raphanistrum* (radish) and many species of *Iris*. Other plants respond in this way to shortened periods of illumination. *Cosmos* and *Nicotiana* flower abnormally early if the daily periods of illumination are short (5–8 hours). Long daily periods of illumination (18 hours) either retard or completely inhibit flower reproduction. Finally, many plants flower and produce seed both under "short-day" and "long-day" conditions. Temperature relations, too, may have an important effect on flower production. Wheat is a "long-day" plant, but in addition to requiring long periods of illumination, some varieties of wheat have their flowering retarded unless at some stage in their development they have been subjected to low temperature. Some (but not all) varieties of rice are " short-day " plants, and have their flowering accelerated by exposure to short days (10 hours). Many of these effects of light and temperature are important economically and explain why some tropical plants fail to flower under the " long-day " conditions of the temperate zone, whilst temperate " long-day " plants do not readily form flowers under the " short-day " conditions of the tropics.

CHAPTER VIII

IRRITABILITY AND PLANT MOVEMENTS

1. Irritability

Irritability is one of the characteristics of living organisms. They are capable of perceiving external stimuli and of responding to them. The responses made are varied, but often under the influence of an external stimulus the plant or a part of it executes a movement. In vascular land plants the movement often takes the form of a bending of the growing region. Some aquatic Algae (p. 443), motile spores and gametes swim in a directed manner under the influence of the stimulus. Not all movements take place because of external stimuli. Other causes operate to produce movements of plant tissues.

2. Plant Movement

We are so accustomed to think of the normal land plant as being fixed in the soil by its root system that the capacity for movement tends to be overlooked. In vascular land plants we get movements exhibited by the protoplasm of single cells, by both mature and growing organs, and less frequently by non-living tissues. With lower plants active movement of the whole plant is frequent. These movements may conveniently be classified as follows:—

A. Living Tissue Movements

(i) **Autonomic movements,** which are apparently spontaneous. Under this heading we include the nutation movements shown by stem apices, which do not grow vertically upwards but follow a spiral course. Of this nature, too, is the protoplasmic streaming seen in the cells of many plants, and the movements of the cilia of motile organisms.

(ii) **Turgor movements** are brought about by changes in turgor. They are shown by some succulent fruits where increasing turgor finally bursts the fruit, so that the juicy contents and the seeds are expelled violently. Turgor changes in the guard cells of stomata are responsible for the movements which result in alterations in the dimensions of the stomatal pores.

(iii) **Stimulus movements**, which may be classified as follows:—

- (*a*) *Tropic movements* (tropisms) are bendings brought about by unequal growth on the two sides of an organ. They are growth movements in which the direction of the movement is governed by the direction of the external stimulus.
- (*b*) *Nastic movements*, like tropisms, are usually growth movements which take place in response to an external stimulus, but the response to the stimulus is not directional. It matters not from what direction the stimulus comes.
- (*c*) *Tactic movements*, unlike tropic and nastic movements, are free locomotor movements of whole organisms and, as would be expected, they are confined mainly to small, generally unicellular aquatic plants. In addition, the reproductive cells of some plants show tactic movements.

B. MOVEMENTS OF NON-LIVING TISSUES

These movements are generally due to shrinkage of tissues on drying. Structural peculiarities result in the tissue shrinking unequally in different directions so that various twists and bends occur.

We will now consider the movements in more detail.

A. (i) Autonomic Movements. The nutation of stem apices is a well marked autonomic movement. In growing, the tips of many and possibly all shoots do not remain in a rigidly vertical position. The apex continually swings round in a circle, *i.e.* it nutates. This nutation is most marked in twining plants, and here it has an obvious biological importance in that it greatly increases the chances of the shoot coming into contact with a suitable support. Nutation is a movement not confined to stems, but sometimes exhibited by leaves also.

Epinasty and hyponasty are two terms used to indicate respectively the more rapid growth of the upper and lower sides of an organ. Epinastic and hyponastic curvatures are often induced but are sometimes autonomic. The fronds of a fern (p. 369) are coiled up in the bud (circinate vernation), and they unfold and straighten as the upper side (inner side of the coiled frond) grows more rapidly than the lower side. This epinastic movement appears to be, in part at least, autonomic. Other autonomic movements that we have mentioned include the streaming of the protoplasm and possibly the undirected swimming of small unicellular aquatic plants.

A. (ii) Turgor Movements. Turgor movements, due to changes of turgor, often result in the violent expulsion of seeds from a containing fruit. An especially good demonstration of this is given by the fruits of the squirting cucumber (*Ecballium elaterium*). In the fruit of this plant the seeds are embedded in a mass of thin-walled tissue which absorbs water. The expansion of these cells is resisted by the thick-walled cells of the fruit wall, and so a high turgor is developed in the fruit. The fruit finally drops off and the high pressure in the centre of the fruit causes the pulp and seeds to be expelled through the weak area left where the fruit separated from its stalk. Turgor mechanisms are responsible, too, for the release of spores in many Fungi; increasing turgor causing spores to be expelled from the ascus in some Ascomycetes, or to be liberated from the sterigmata in many Basidiomycetes (Chap. XX). The importance of turgor changes in controlling the movements of the guard-cells of the stomata, and hence in regulating the dimensions of the stomatal pore has already been pointed out.

A. (iii) Stimulus Movements. Stimulus movements, as already indicated, fall into three main classes, *viz.* tropic, nastic and tactic.

(*a*) *Tropic movements.* Many external stimuli exert an influence on the direction of growth. This is well seen with plants grown in windows where the unequal illumination results in the stem of the plant bending in the direction of maximum illumination. This is a *phototropic* movement, and as the bending is towards the source of the light it is said to be a *positive phototropism,* and is a feature generally exhibited by stems. A similar plant placed in a horizontal position and illuminated equally from all sides soon shows an upward curvature. Under the influence of gravity the shoot grows upwards. It is *negatively geotropic.* Roots, on the other hand, are *positively geotropic* (Fig. 162), and sometimes *negatively phototropic.* Many roots, however, are insensitive to one sided illumination, and do not exhibit phototropic curvature.

The *phototropic curvatures* of stems depend on a number of factors. The curvature does not take place over the whole length of the stem, but is confined to the growing region, especially to the part just behind the tip where rapid cell extension is taking place. The mechanism of these curvatures has been extensively studied with the coleoptile of the seedling of the oat (*Avena sativa*, see p. 210 and Fig. 161). This organ is very sensitive to light (and also to gravity). When in a dark box which has a slit at one side so that the seedlings receive illumination from one side only, a curvature towards the slit may be observed within an hour from the beginning of the one-sided illumination. The curvature normally takes place some distance behind the tip. If the tip of the coleoptile is removed or covered by a small tinfoil cap, one-sided illumination no longer produces a phototropic response. Clearly the tip is the region where the stimulus is received, and the excitation then passes backwards to the region where the curvature takes place. The effect of the one-sided illumination is to alter the distribution of auxin in the coleoptile. On the shaded side the concentration of auxin is greater than on the fully-illuminated side. Downward diffusion of auxin from the tip takes place most readily on the shaded side and so we get, on the shaded side, accelerated cell extension with the result that the coleoptile bends towards the source of light.

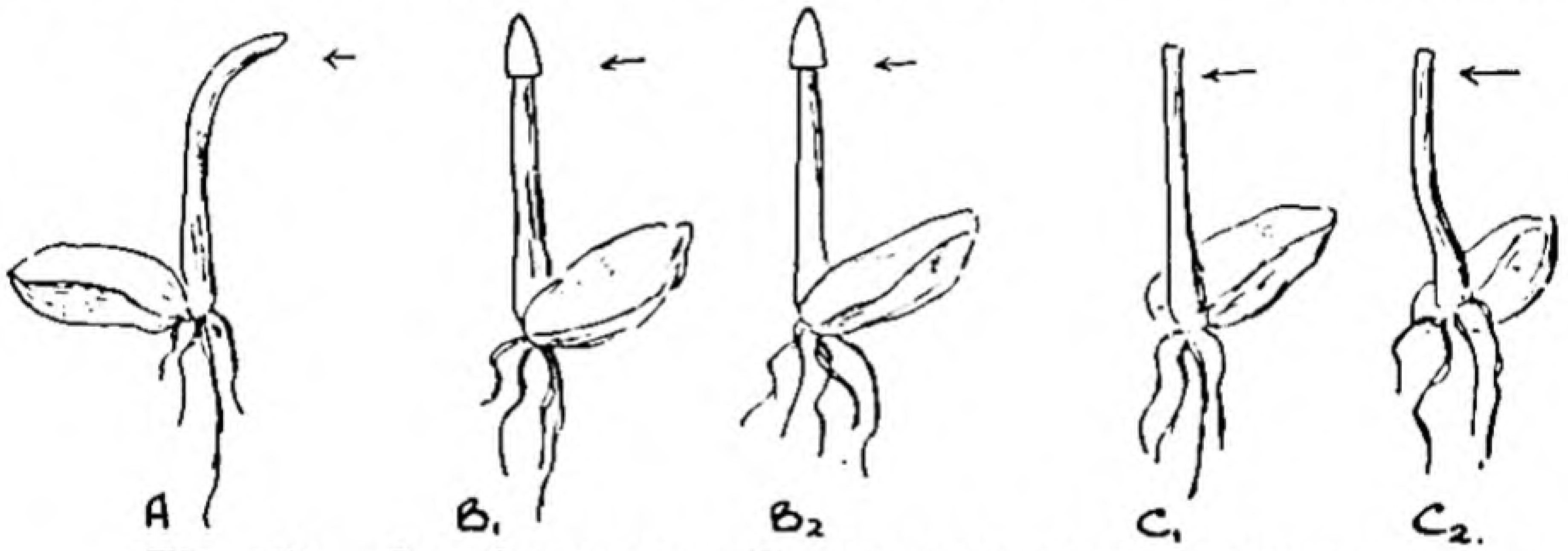


Fig. 161. Oat Seedlings. Experiments to show Site of Perception of Light Stimulus.

A, Normal positive phototropism; B_1, Tinfoil cap over apex of coleoptile; B_2, The same seedling after unilateral illumination; C_1, Apex of coleoptile removed; C_2, The same, after unilateral illumination. The arrows show direction of incident light.

The phototropic response is conditioned by many factors. The intensity of the illumination is important, the response being more marked at higher light intensities, up to a point. If the light is too intense a negative phototropic curvature sets in, but the reasons for this are obscure. As the curvature is a growth movement it occurs most readily when conditions are favourable for growth, *i.e.* when the supplies of water and oxygen are abundant. Phototropic curvatures in shoots other than the *Avena* coleoptile are probably of a similar nature, being brought about by an unequal distribution of auxin consequent upon the unilateral illumination, but in some dicotyledonous shoots, where the growing zone is longer than in the *Avena* coleoptile, the region of curvature is also longer. Stems, because of their positively phototropic reaction, tend to arrange themselves parallel with the incident light rays. Most leaves, on the other hand, arrange themselves at right angles to the light rays, and are said to be diaphototropic or plagiotropic. They are able to twist, usually by means of the petiole, so that if the direction of the light is altered the leaves undergo a corresponding movement. The biological advantages of these movements is obvious. Shoots in nature grow towards the source of light. This combined with the plagiotropic movements of the leaves ensures adequate illumination of the photosynthetic tissues.

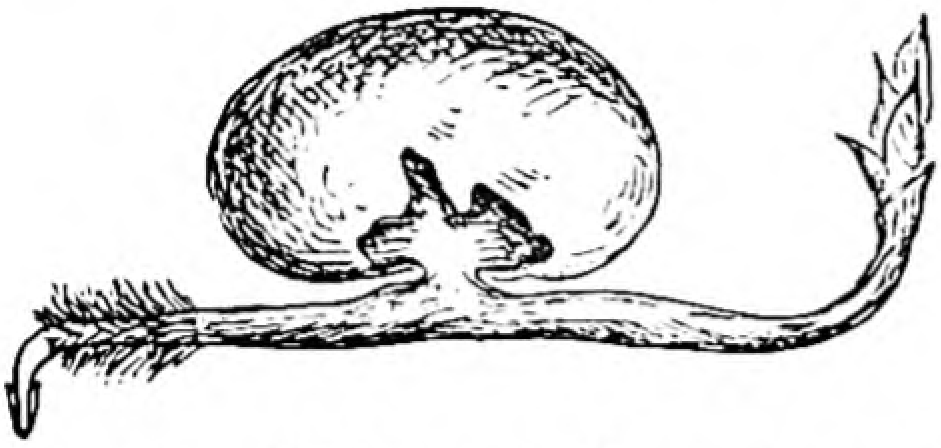


Fig. 162. GEOTROPIC CURVATURE OF SHOOT AND ROOT OF SEEDLING LAID HORIZONTALLY.

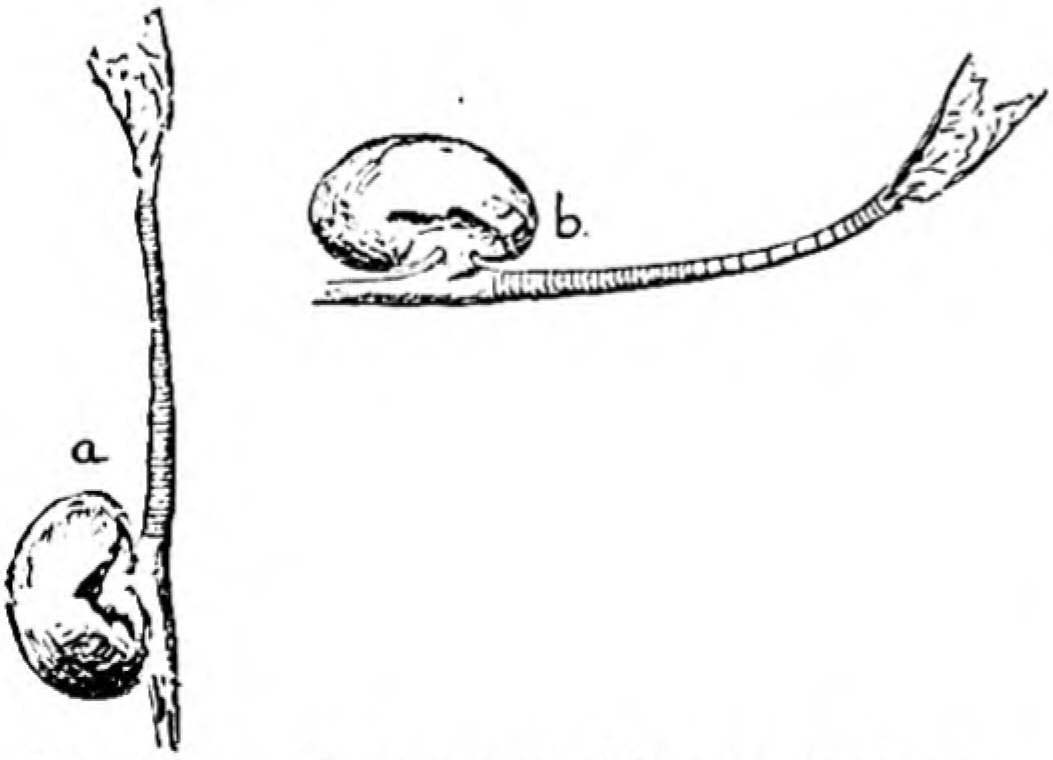


Fig. 163, A. REGION OF CURVATURE OF STEM MARKED IN MM. AND LAID HORIZONTALLY.

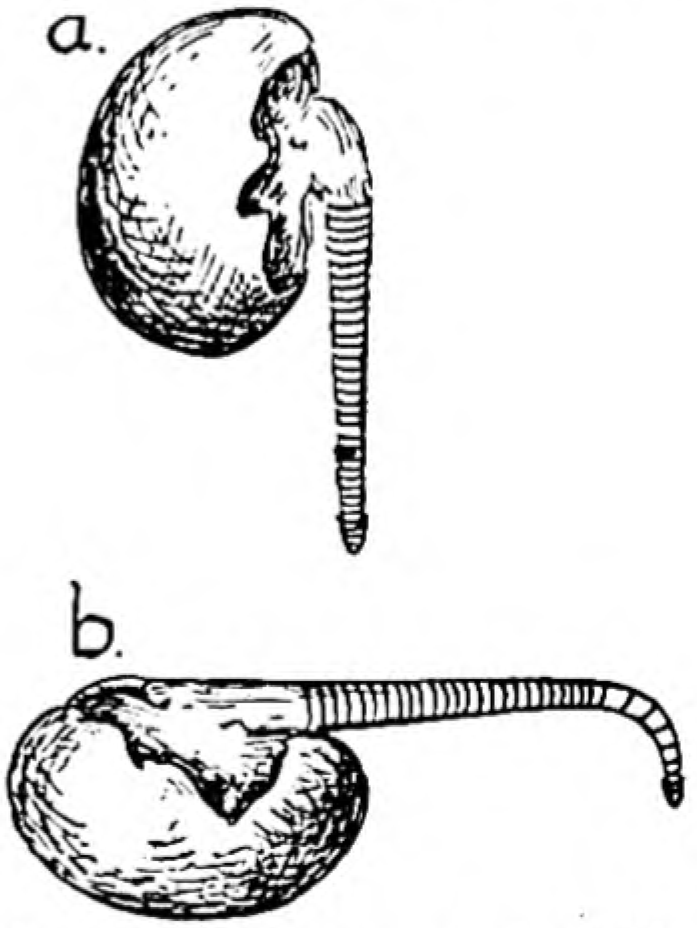


Fig. 163, B. REGION OF CURVATURE OF ROOT MARKED IN MM. AND LAID HORIZONTALLY.

Geotropic movements are of a similar nature to phototropic curvature. When placed in a horizontal position and illuminated equally from all sides shoots bend upwards and roots downwards, the former being negatively, the latter positively geotropic. That gravity does induce these curvatures can be shown by the use of an apparatus known as a Clinostat. In essence this is a clockwork mechanism which will slowly rotate a pot or other holder containing a plant. Slow rotation in a horizontal plane eliminates the unilateral effect of gravity, and the shoot and root grow in an undirected manner. By rapid rotation not only is the effect of gravity eliminated, but the seedlings are subjected to a centrifugal force of some magnitude. That is, gravity is replaced by centrifugal force directed radially outwards from the rotating axis. Under these conditions we find that the roots of seedlings grow outwards (*i.e.* in the direction of the centrifugal force), whilst shoots grow in the opposite direction. The seedlings react to a centrifugal force just as they do to gravity.

Geotropic curvatures, like phototropic ones, are growth movements, and in like manner the curvature is restricted to the growing zone of the organ (Fig. 163). When a shoot or root is placed in a horizontal position auxin accumulates on the lower side. The greater concentration of auxin on the lower side of the shoot accelerates cell extension in this region so that an upward bending occurs. In the root the increased concentration of auxin on the lower side has the effect of retarding cell extension, and so here the greatest rate of growth is shown by the upper-side, so that a downward bending takes place. Some shoots are diageotropic, and arrange themselves at right angles to the pull of gravity, that is, horizontally. Examples are furnished by the rhizomes and runners of many plants, e.g. *Adoxa, Scirpus.*

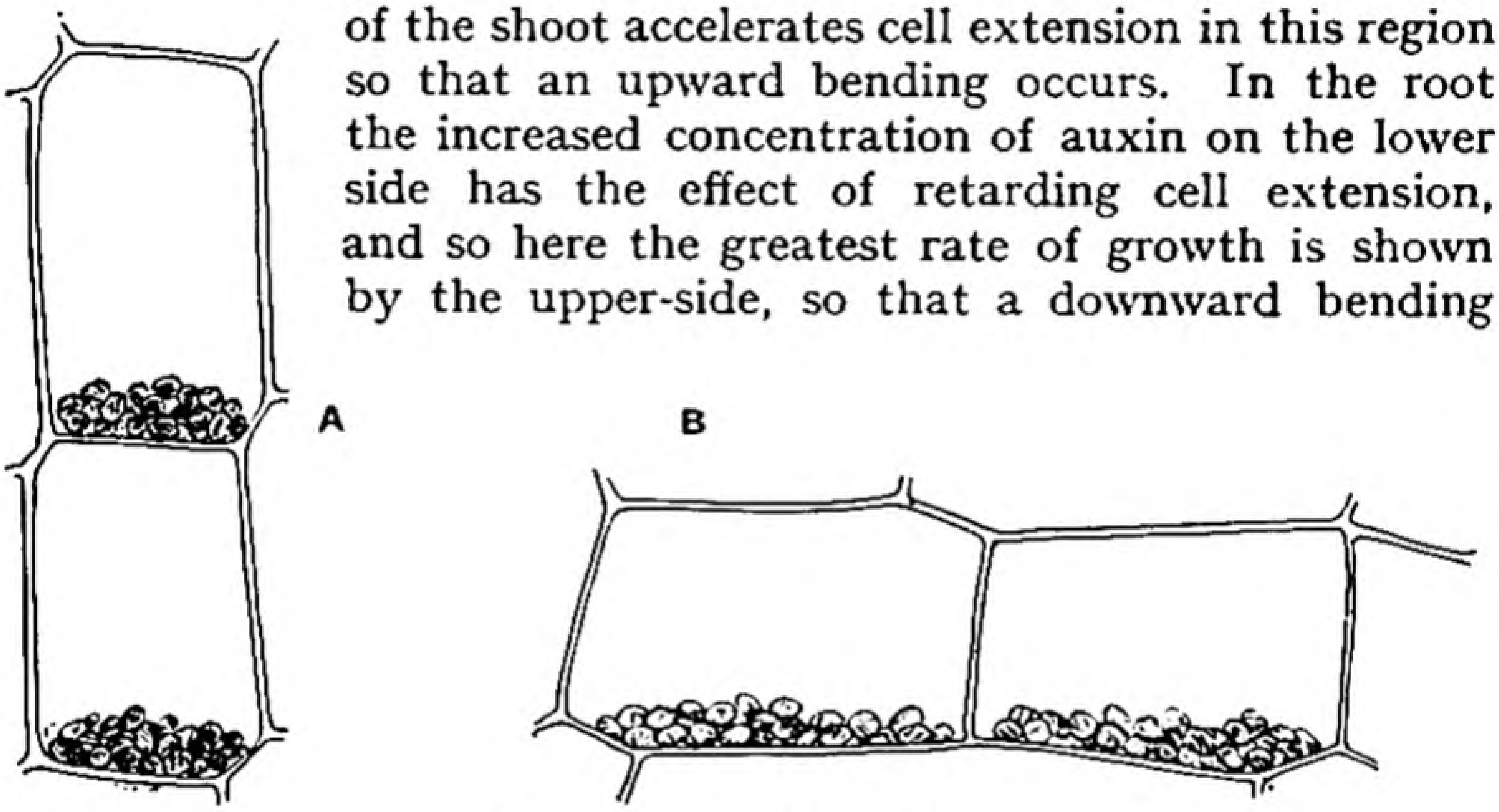


Fig. 164. STATOCYTES.

A, In the Root-Cap; B, The Endodermis.

Although it is generally believed that geotropic curvature takes place in response to a gravity-induced redistribution of auxin in displaced organs, mention must be made of the *statolith theory.* According to this the stimulus of gravity is perceived by certain movable starch-grains in certain cells of the plant. Starch-grains (statolith starch) which do move are without doubt present in the endodermis (starch-sheath) of many stems, and in many of the cells near the root-tip (e.g. root-cap, Fig. 164). The cells containing these movable starch-grains are termed statocytes, and normally the statolith-starch rests on the morphological (and actual) lower side of the cell. If a shoot or root is placed in a horizontal position, the statolith-starch-grains slowly fall under the influence of gravity, until they rest on the morphologically lateral (now the lower) walls of the statocytes. This is supposed to constitute a stimulus which is transmitted to the actively growing region and causes the organ to bend in such a way that the statocytes (and hence the organ) are returned to their original and normal position. We cannot say if this view is at all correct, but it is noteworthy that in general, sensitivity to gravity is most marked where the statolith apparatus is well developed. As with phototropic movement so with many geotropic curvatures, their biological advantages are clear. Negative geotropism of the shoot may, in part, determine the upward course of the young shoot of germinating seeds buried in the soil, and hence removed from the effect of light. It helps to ensure rapid regaining of the vertical position when shoots of growing plants have suffered displacement by wind or from other causes.

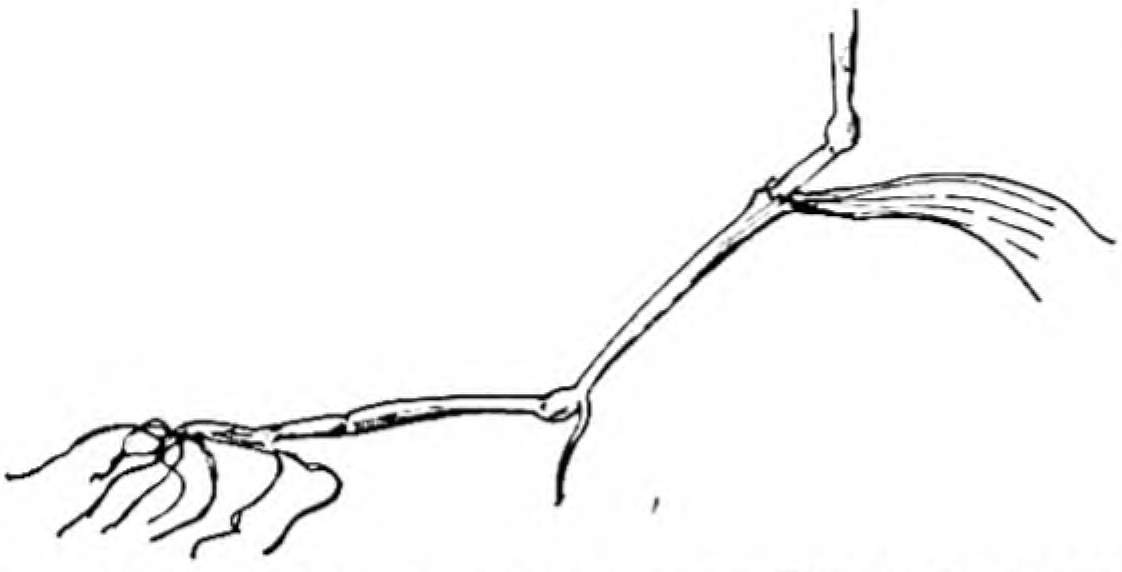


Fig. 165. STEM OF GRASS LAID HORIZONTALLY BENDS UPWARDS BY UNEQUAL GROWTH AT THE NODES.

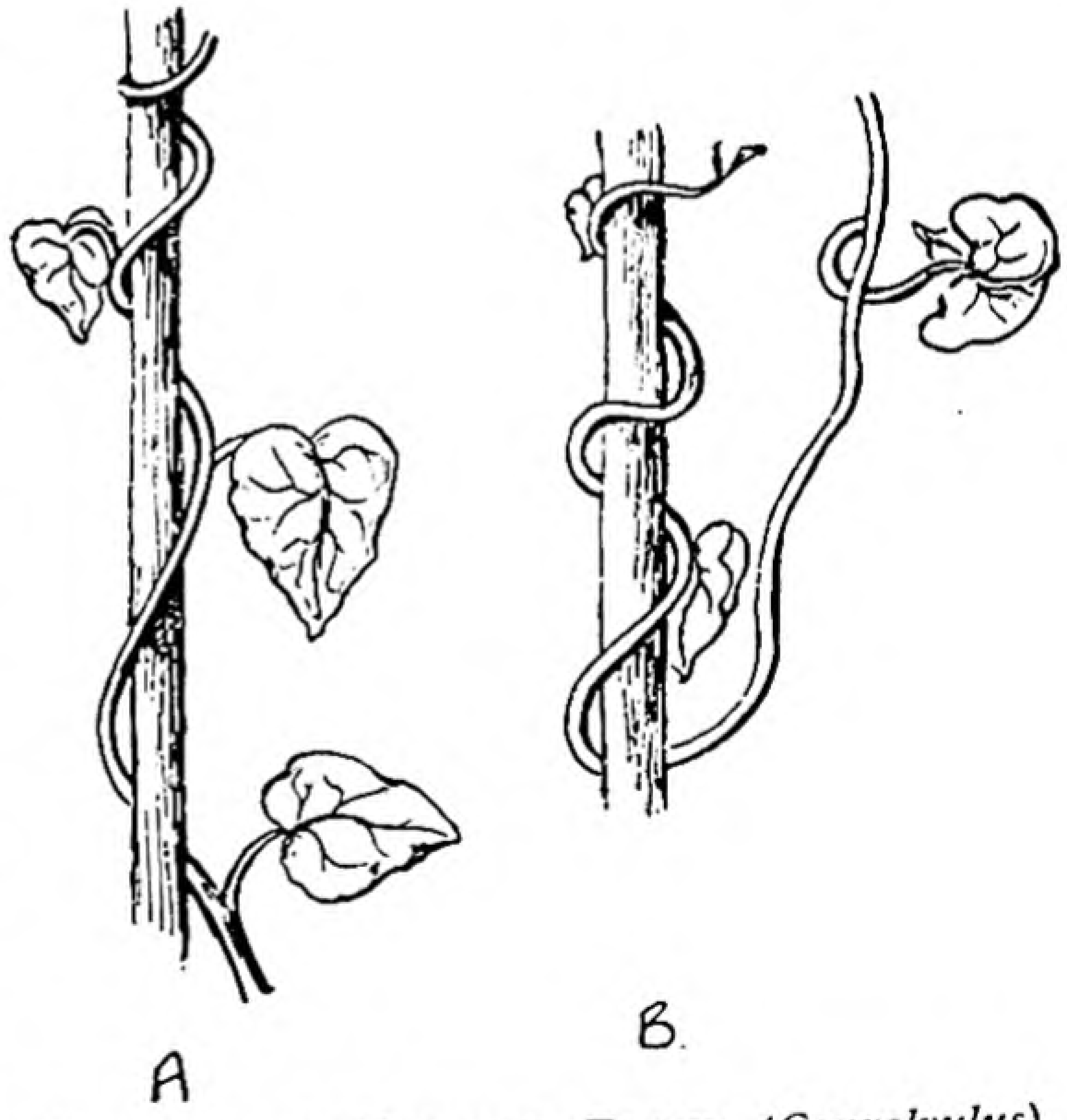


Fig. 166. A TWINING PLANT (*Convolvulus*). A, Normal; B, Inverted.

We have pointed out that the geotropic curvatures exhibited by shoots take place in the growing zone. Exceptions to this rule are furnished by the stems of most grasses (Fig. 165) and of certain *Dianthus* species. Here the curvatures are executed by the nodes, and the ability to bend is retained long after shoot elongation has ceased. The result is that if the shoots of these plants are placed in a horizontal position they return to the vertical position from one or more points near the base of the shoot. Gravity here induces growth in the lower side of an already mature node so that an upward bending occurs.

The twining movement of many climbing plants (Fig. 166) is related to gravity. In these plants the nutation of the shoot tip is very marked. The tip swings in a circle either in a clockwise or counter-clockwise direction. This direction is always the same for a given species of plant. If in the course of this movement it encounters a vertical support, it twines around it. The importance of gravity in this twining is well shown if a plant which has twined around a vertical support is inverted. The last two or three coils of the stem untwist and straighten out. The tip at first becomes erect, then nutates and twines around the support still in the clockwise or counter-clockwise direction, but, of course, now forming a coil opposite to that of the inverted position of the plant. There is here a clear indication of the importance of gravity, but the exact rôle of gravity and the extent to which autonomic movements are important in the physiology of twining cannot be stated.

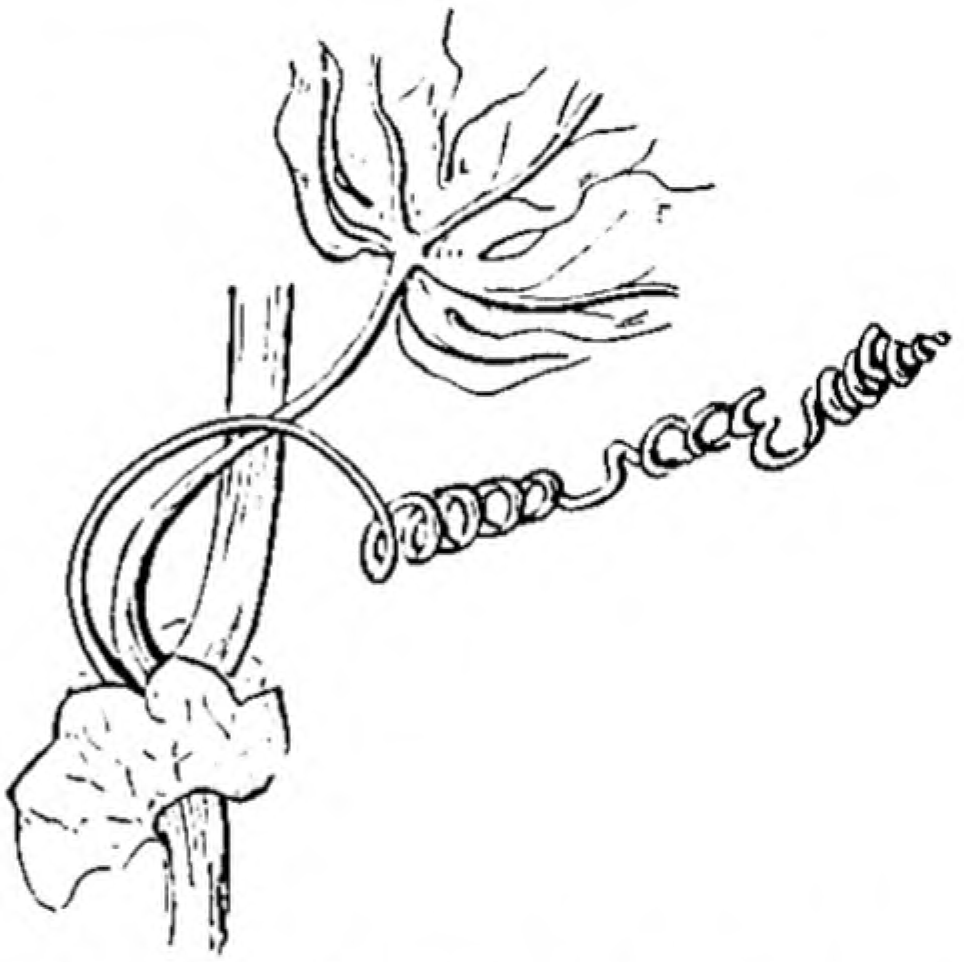


Fig. 167. TENDRIL OF *Passiflora*.

Haptotropism or *Thigmotropism*, denoting a response to contact stimulus, is exhibited most markedly by tendrils (Fig. 167). The morphological nature of tendrils is varied (pp. 84, 137), but they are nearly all sensitive to contact stimuli. In *Passiflora* (passion-flower), the tendril, when young, is spirally coiled, with the lower side outwards. It later straightens and its tip nutates. This is probably an autonomic movement. The apical part of the tendril is sensitive, and if rubbed or touched by a solid body, especially if the surface is rough, it bends towards the stimulated side. The bending may take several minutes. But in *Momordica cochinchinsis* (Family Cucurbitaceae) it is evident in less than one minute after stimulation. The bending results in a fresh part of the tendril coming into contact with the solid object, and so the stimulation is continuous; the tendril continues to bend, and by so doing encoils the support. The coiling around the support is a growth movement.

Contact with a solid body accelerates growth in these sensitive organs on the side of the tendril remote from the point of contact. Contact with drops of liquid, even of a heavy liquid like mercury, does not produce bending. When the apical part of the tendril has coiled around a twig or other support a secondary reaction of the tendril takes place. The basal part of the tendril twists spirally in the reverse direction from the apical coil, and the stem of the climber and the support are drawn closer together. The spiral twisting, too, increases the elasticity of the tendril. One result of this is that the stem of the plant and the support can move in the wind with little risk of the tendril snapping.

Response to contact stimulus is shown by plants other than tendril climbers. We have already pointed out that the marginal tentacles on the leaf of *Drosera* (p. 201), when stimulated by contact, tend to bend inwards, so that an insect trapped in the sticky secretion of the hairs is effectively imprisoned. The slightest touch given to one of the sensitive bristles (trigger-hairs) on the leaves of *Dionaea muscipula* (Venus' fly-trap) causes the two halves of the leaf to close together rapidly (p. 202).

Chemotropism, growing or bending towards chemical substances, is a widespread phenomenon especially well-shown by many Fungi (p. 471) which grow towards such nutritive substances as peptone and asparagin. The growth of pollen tubes in the stigmas of flowers (p. 267), too, is a directed growth, the direction probably being due to chemical substance in the stigma.

The marginal tentacles of *Drosera* (Fig. 168) show curvature in response to chemical stimuli (chemotropism) as well as to mechanical stimuli (haptotropism). In nature probably both operate. If an insect is caught in the sticky secretion of a marginal tentacle, the latter bends inwards, with the insect, towards the shorter tentacles, and when these are touched the stimulus is transmitted to neighbouring marginal ones which also bend over the insect. Some time after the reception of the stimulus causing curvature, a straightening of the tentacles takes place by a reverse curvature. Curvature may be induced by a blow with a pencil, by contact with any solid substance, or by chemical substances such as ammonium salts, phosphates and proteins (white of egg, raw meat, etc.). It should be noted that these movements of *Drosera* tentacles are not entirely directed movements. To a great extent the direction of the movement is independent of the direction of the stimulus. They partake of the character of nastic movements.

Hydrotropism is a special form of chemotropism, and the radicles of seedlings especially, show a positive hydrotropism, growing towards regions of higher humidity. The hypocotyls of seedlings, on the other hand, are frequently negatively hydrotropic and grow away from regions of high humidity, and a similar negative hydrotropism is shown by the reproductive organs ot some Fungi.

(*b*) *Nastic Movements*. The above directed tropic movements contrast with *Nastic* movements where the movement is caused but not directed by the external stimulus. The opening and closing of many flowers are nastic movements, and nastic movements induced by both light and temperature changes are common. If the flowers of the crocus (*Crocus verna* and *C. lutea*) when in an unopened state are subjected to a temperature increase of from ten to fifteen degrees, they pass from the closed to the completely open state in a few minutes. The opening is due to a relative increase in growth rate on the inner side of the petals. A sudden fall in temperature has the reverse effect, causing a relative decrease of the growth rate on the inner side of the petal so that the flower closes. In these cases the temperature stimulus is received generally, but the movement takes place in a particular direction. The movement is caused, but not directed by, the stimulus. It is a *thermonastic* movement. *Photonastic* movements are shown by the capitula of *Calendula officinalis* which open on exposure to light and close when darkened. Many flowers exhibit similar photonastic movements, but the commonly observed diurnal opening and closing of flowers and other organs are not always due to this cause. There is in some an inherent tendency to open and close in a definite rhythm, which is exhibited even in the dark. The leaves of *Oxalis*, for instance, show daily movements when in the dark (Fig. 169).

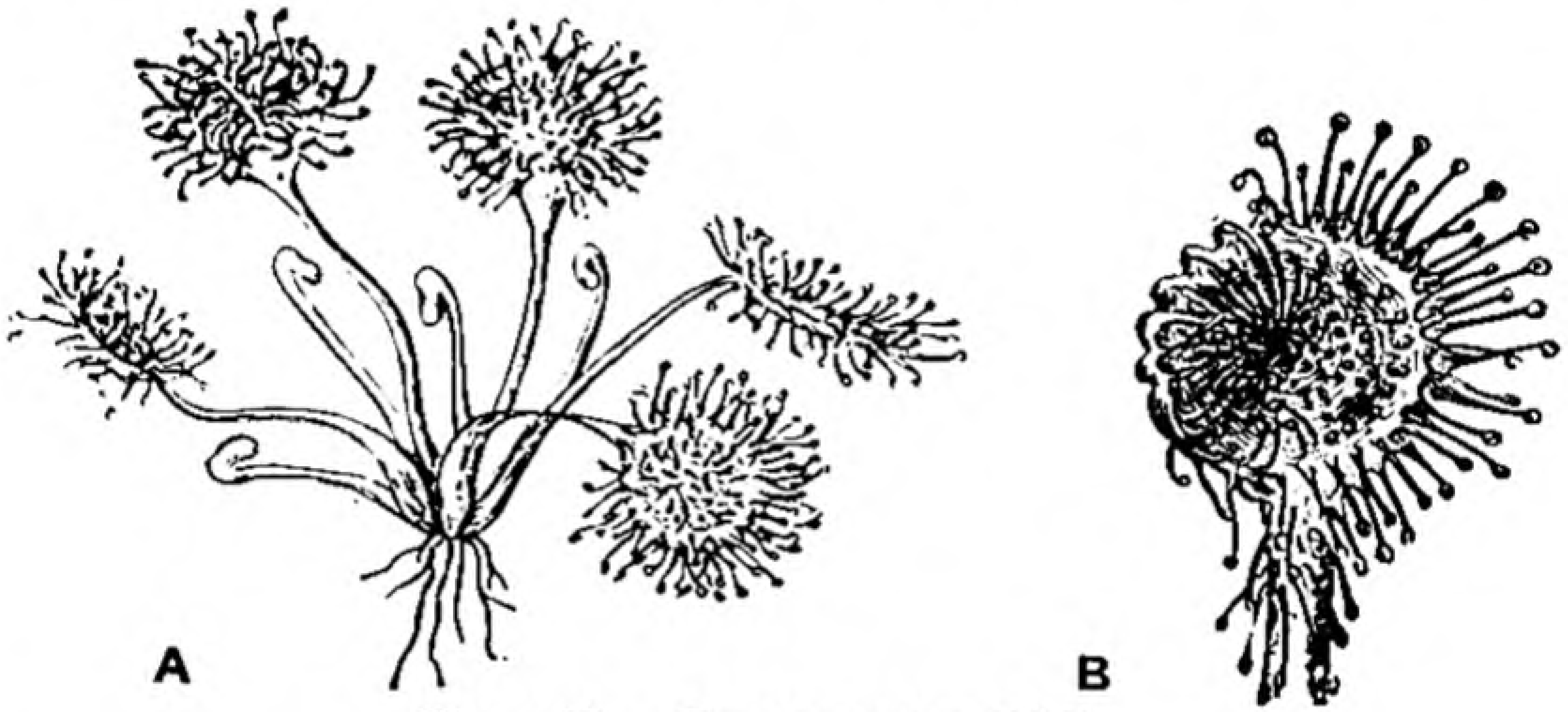


Fig. 168. *Drosera rotundifolia*.
A, Plant; B, Leaf with tentacles closed over captured insect.

Photonastic movements of leaves are of common occurrence, but the photonastic response is generally affected by other factors. Many compound leaves assume a characteristic position at night, which is very different from their daytime position. This night-time alteration of position — the sleep, or *Nyctinastic* movements—results generally in a folding up of the leaflets. In some acacias, these movements seem to be photonastic, the leaflets folding together when the leaf is darkened. With many other plants the assumption of the night position of the leaves normally coincides with the onset of darkness, but the movements continue if the plant is kept continually dark. Here the movement clearly is autonomic. The sleep position in which the leaflets fold together and in which the leaf frequently assumes a vertical position is generally then, not the result of a simple photonastic movement. In *Mimosa pudica* (Fig. 170), in the sleep position, the leaflets are all folded together and the whole leaf hangs down, and this position is commonly assumed during the evening. It can, however, be brought on at any time during the day if the plant is subjected to the stimulus of shock. Shaking the plant induces it, or the singeing of a single leaflet may suffice. The movement is rapid, and in a

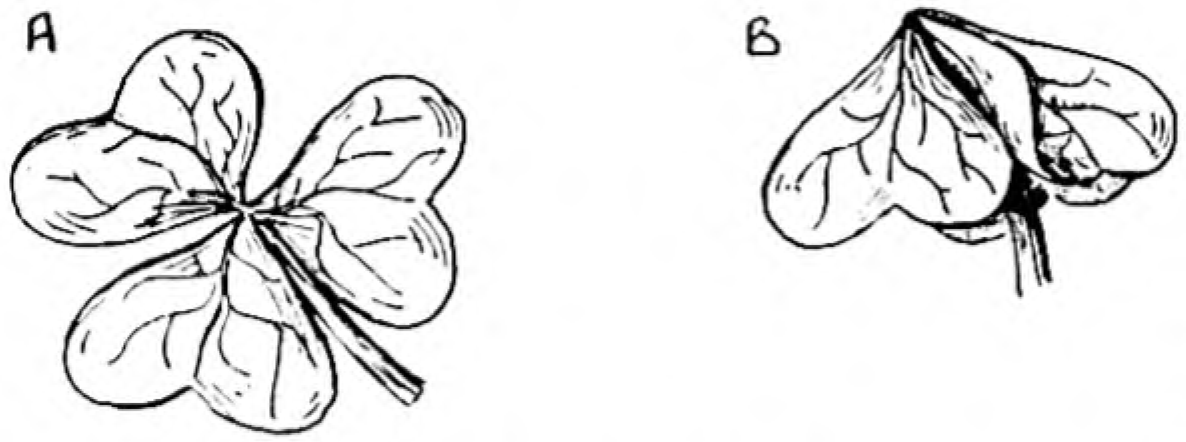


Fig. 169. *Oxalis* LEAF.
A, Normal; B, Sleep position of leaflets.

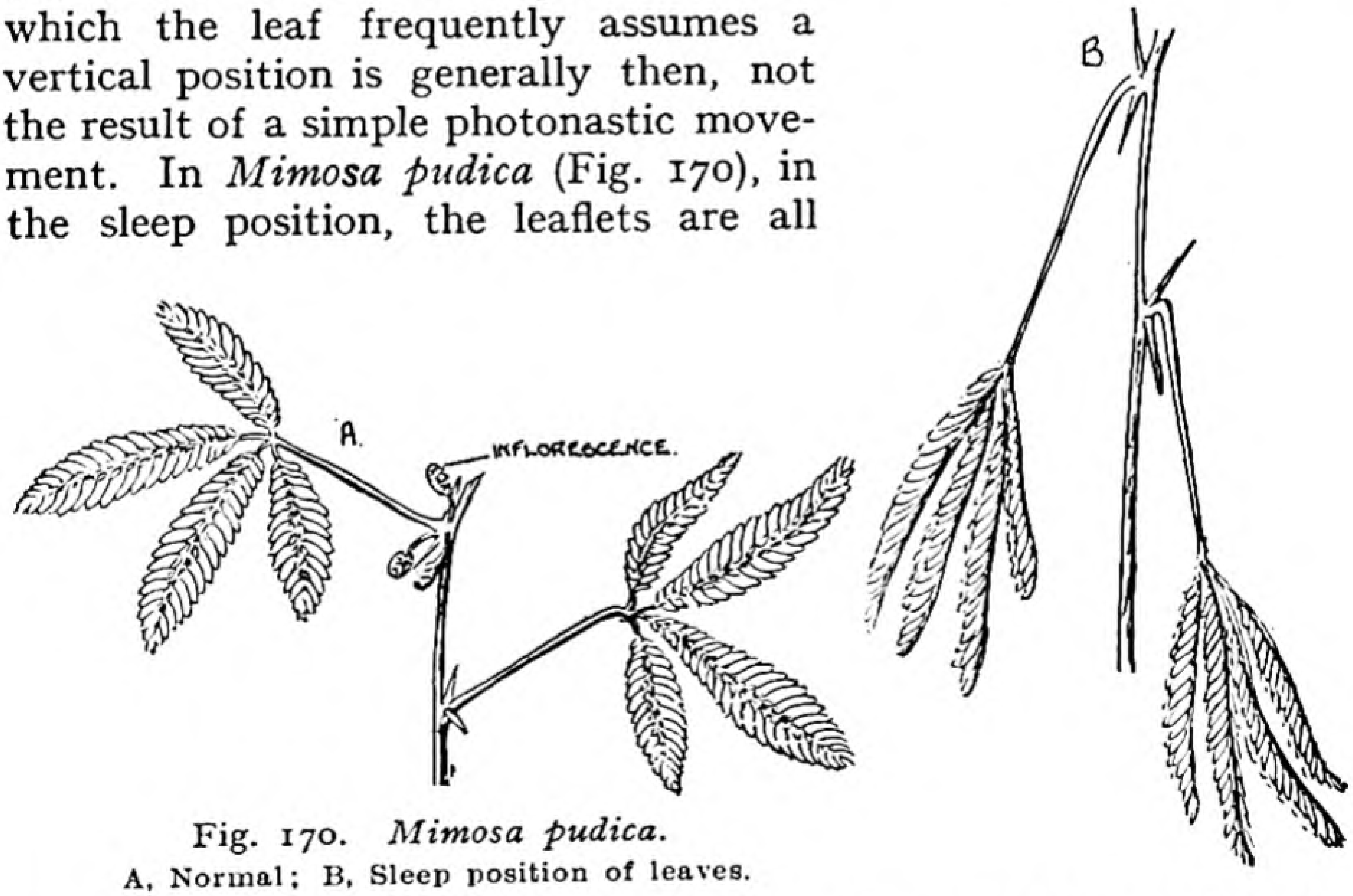


Fig. 170. *Mimosa pudica.*
A, Normal; B, Sleep position of leaves.

few seconds after the stimulation the plant will have assumed the night position. Movements which take place as the result of shock stimulus are referred to as *seismonastic movements*. Many of these nastic movements are biologically important. The thermonastic and photonastic response of many flowers ensures that they open only in warm, bright weather. At night, or when the temperature is low, they remain closed, and the reproductive parts of the flower are protected. The nyctinastic movements of many leaves protect the stomata at night. Blocking of the stomata by dew is prevented, and so transpiration commences early in the morning when the leaves unfold. It is easy to overstress the significance of these movements. It is well to realise that many plants do not exhibit them and yet do not appear to suffer on this account.

(*c*) *Tactic movements*. These movements are generally movements of whole organisms. They are directed movements and are shown most commonly by unicellular structures. Tactic movements are usually brought about by cilia or flagella and may occur in response to various external stimuli. *Phototactic* and *Chemotactic* movements are the commonest movements of this type. Phototactic movements are exhibited by many unicellular Algae (e.g. *Chlamydomonas*, p. 443), which swim freely in water. The direction of swimming may be governed by the direction of the illumination. If the plants are subjected to illumination they swim towards the source of light and they are said to be positively phototactic, but they exhibit negative phototaxis if the illumination is too intense. As a result of this they place themselves in such a position that photosynthesis is promoted, whilst damage to the chlorophyll is avoided. Of a somewhat similar nature are the movements of chloroplasts that take place within the green cells of many plants. The chloroplasts exhibit phototaxis, and in light of moderate intensity they arrange themselves with their "flat" side fully exposed to the source of light, so as to receive the maximum amount of illumination (epistrophe position). When the light is too intense they place their edges towards the light so that excessive illumination is avoided (apostrophe). These movements

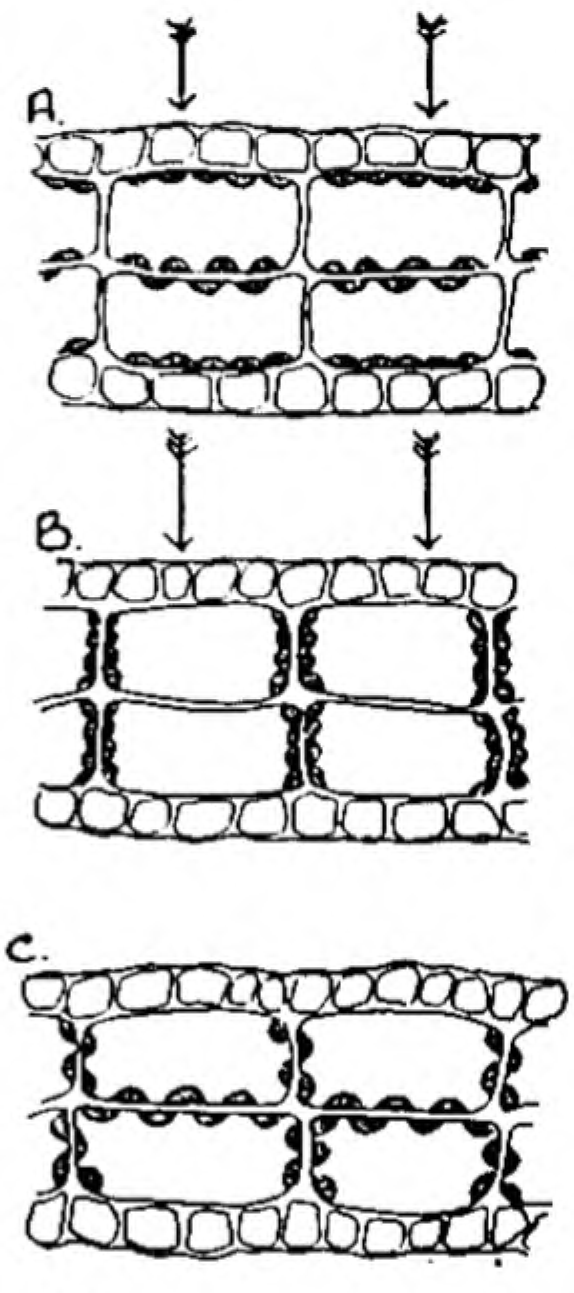


Fig. 171. CHLOROPLASTS OF *Lemna*.
A, In diffuse light; B, In bright light; C, In darkness.

are shown very well in many Algae, in the thin " leaves " (really flattened stems) of *Lemna* (duckweed, Fig. 171), and in the palisade cells of the leaves of other Angiosperms.

Chemotactic movements are exhibited chiefly by Bacteria and by motile gametes. Bacteria commonly show positive chemotaxis in relation to substances which can constitute food materials for them (e.g. peptone, asparagin, dextrose, lactose), and swim from a region of low to one of higher concentration. They show negative chemotaxis in relation to many toxic substances.

One or both gametes of many plants are provided with cilia which enable them to swim freely in water. They are chemotactic and respond to certain chemical substances. The female reproductive organs commonly produce substances which attract the spermatozoids chemotactically. Many ferns, for instance, produce malic acid in their archegonia, which depend on water for fertilisation. The malic acid, which is soluble, diffuses into the water from the neck of the archegonium and spermatozoids swimming in the neighbourhood come into a zone with a low concentration of malic acid. They are positively chemotactic to this substance and so swim from the region of low to the region of higher concentration. In this way they reach the neck of the archegonium, and one spermatozoid, swimming down the neck, fertilises the ovum. The spermatozoids of mosses are sensitive to sugar. These chemotactic movements of reproductive cells are common, and their importance will be better realised when Chaps. XIV, XVIII and XIX have been studied.

Aerotaxis, shown by many Bacteria which swim to regions where the oxygen concentration is relatively high, is a special case of chemotaxis.

B. MOVEMENTS OF NON-LIVING TISSUE. These are usually brought about by unequal shrinkage as the result of drying. The unequal shrinkage may be due to differences in the structure of the cell-wall of one row or layer of cells, or to differences in structure and arrangement of two or more layers of cells. As examples of the former may be cited the sporangium-wall of ferns, the peristome of moss capsules, and the anther-wall of Seed Plants; of the latter the pericarp of gorse (*Ulex*) and other fruits. These and many other examples, are dealt with in more detail in Chapters XII, XIV, and XVIII.

CHAPTER IX

STRUCTURE OF THE FLOWER

1. General

The flower may be regarded as a leafy shoot highly specialised for the performance of reproductive functions. The function of a flower is to produce seed and fruit, and the various parts (stem and leaf organs) are specially suited to the performance of that function. The essential structures in the flower, therefore, are the organs, which are more immediately concerned in the production of seed. We cannot appreciate the significance or morphological nature of the organs without a knowledge of the reproductive organs of the Vascular Cryptogams and Gymnosperms, and some of the terms used in this chapter will only be understood when these plants have been considered.

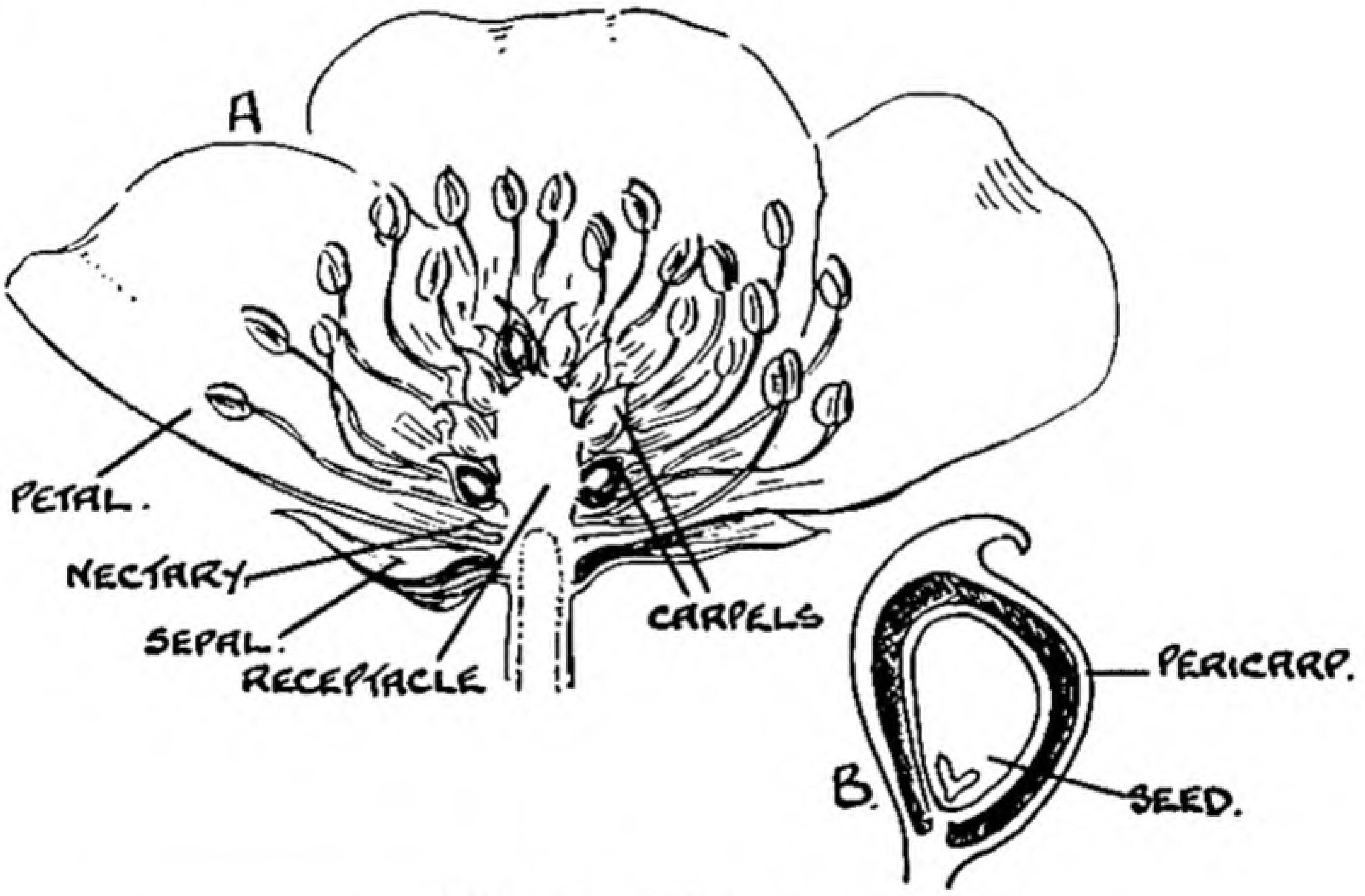


Fig. 172. BUTTERCUP.
A, Longitudinal section, Flower; B, Longitudinal section, Achene.

The axis (stem portion) of the flower usually shows two regions—the **pedicel**, and the **receptacle**. The pedicel is, popularly, the stalk of the flower. It may be present or absent. If present, the flower is *pedicellate*; if absent, *sessile*. The receptacle is the portion of the axis to which the floral leaves are attached. In many flowers there are four sets or series of floral leaves. To the outside are the **sepals**; collectively, they constitute the **calyx**. Internal to these are the **petals**, constituting the **corolla**. Then come the **stamens** forming the **androecium**; and finally, in the centre of the flower, are the **carpels**, forming the **gynaeceum*** or **pistil**.

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* *Gynaecium* and *gynecium* are varieties of spelling in common use.

The buttercup (*Ranunculus*) flower will serve as a convenient type for introduction to these structures (Fig. 172). In the buttercup the carpels are separate from each other, and *each* shows a hollow basal portion called the **ovary**, above which are the parts known as **style** and **stigma** (Fig. 172, B). In many flowers the carpels are united and form a single ovary (see Fig. 185).

The following facts support the above view of the morphological character of the flower: (*a*) the flower, like an ordinary foliage-shoot, arises as a bud, very often in the axil of a leaf (*bract*). (*b*) The receptacle has the general structure of a stem, and the sepals and petals in their structure and development resemble leaves. (*c*) While in most cases the stamens and carpels are quite unlike leaves, there are certain conditions in which they become distinctly leaf-like. Thus, in many cultivated flowers, e.g. rose, the stamens are transformed into petals; in double cherry the gynaeceum is represented by a tuft of small green leaves; in water lily there is a gradual transition between petals and stamens.

2. The Inflorescence

The floral, or reproductive region of the plant is usually distinctly marked off from the foliage, or vegetative region, and is known as the **inflorescence.** Sometimes the main vegetative-axis of the plant ends in a single terminal flower, e.g. tulip and wood anemone. Here the flower is said to be **solitary** and **terminal.** In other cases, the flowers are developed singly in the axils of ordinary foliage leaves, and are called **solitary** and **axillary.** These are simple types of inflorescence. Usually the flowers are aggregated on a more or less complex branch-system. According to the nature of the branching, and other features, many different kinds of such inflorescence are recognised. These will be specially considered later (Chap. X).

The main or primary axis of the inflorescence, together with any secondary axes which may be developed (apart from the pedicels of the flowers), is called the **peduncle.** This term is applied instead of pedicel to the stalks of solitary terminal, and solitary axillary flowers. If the peduncle is an unbranched leafless axis which arises from the midst of radical leaves and bears flowers at its apex, it is called a **scape,** e.g. cowslip and members of the Amaryllidaceae.

3. Bracts, etc.

When the flower arises as a lateral bud, the axis on which it is borne is called the **mother-axis.** This may or may not be the primary axis of the inflorescence. The side of the flower which is towards the mother-axis (or towards the growing point of the mother-axis) is said to be **posterior**; the side away from the mother-axis is **anterior.** In a solitary terminal flower it is evident that these terms are not applicable.

If the flower arises in the axil of a leaf-structure, this leaf-structure is called a **bract.**

Bracts present great variety of form and colour. The bracts may be ordinary foliage leaves, as in solitary axillary flowers, or may more or less differ from them. Frequently they are small, green, and scale-like. In many plants they are reduced to small, tooth-like structures. When they are not green, but coloured like the petals of a flower, they are said to be *petaloid*. In many flowers the flower-stalk bears small out-growths of the nature of reduced leaves. These are called **bracteoles.** When present, there are *usually* two in Dicotyledons, placed laterally, and one in Monocotyledons, situated on the posterior side.

4. Perianth

The outer series of floral leaves, distinct from stamens and carpels, constitute the perianth. Flowers without perianth are naked or **achlamydeous.** Flowers with a single perianth series are **haplo-** or **monochlamydeous** and the floral leaves (tepals) are either bracteoid or petaloid. Flowers with a double perianth (two series of floral leaves) are **diplochlamydeous.** When both series of floral leaves (tepals) are similar they are **homoiochlamydeous,** but fusion of the two series may render them apparently haplochlamydeous. When the two series of floral leaves are dissimilar, **heterochlamydeous,** the outer series is sepaloid (sepals, calyx) and the inner series petaloid (petals, corolla). When petals are absent as a result of abortion the flower is **apopetalous.**

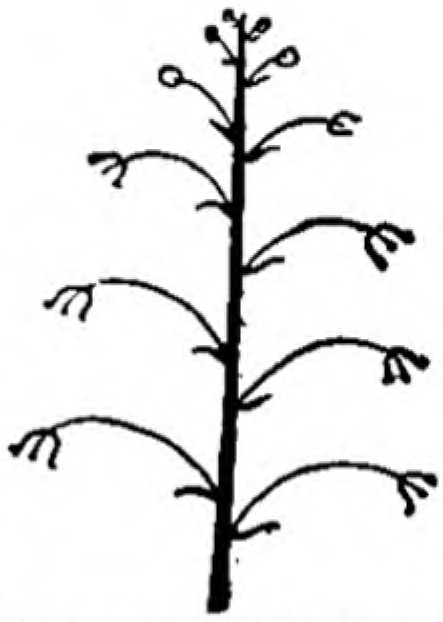


Fig. 173. DIAGRAM OF RACEME.

5. The Essential Organs

The androecium and the gynaeceum, because they bear the reproductive bodies, microspores (pollen-grains) and ovules, necessary for the production of seed, are called the essential organs.

If both are present *in the same flower* (the rule in Angiosperms) the flower is hermaphrodite or *bisexual* (symbol ☿). When they are borne on different flowers, as is sometimes found, the flowers are imperfect or *unisexual*. The unisexual flowers bearing the stamens are male (♂) or *staminate*; those bearing carpels, female (♀) or *pistillate*. If staminate and pistillate flowers are borne on the same plant (e.g. hazel), the plant is **monoecious**; if on different plants (e.g. willow and some species of campion), **dioecious.** A plant is *polygamous* if it bears staminate, pistillate, and hermaphrodite flowers (e.g. *Fraxinus*, *Mangifera*, *Anacardium*, *Rhus*, etc.). Flowers in which both stamens and pistil have been lost are *neuter* (e.g. ray florets of *Senecio* species, *Volutarella*, *Helianthus*).

6. Floral Phyllotaxis

In most flowers the series of floral leaves are arranged in whorls, and the phyllotaxis is *cyclic*. Sometimes, however, all the floral leaves are in a spiral (e.g. cactus) and the flower is said to be *acyclic*. If some of the series are cyclically arranged, others spirally, the flowers are *hemicyclic*. In buttercup, for example, the calyx and corolla are whorled, while the stamens and carpels are spiral.

7. Number of Parts

In general, then, flowers have four definite series of floral leaves—calyx, corolla, androecium and gynaeceum—often with the same number of parts in each series. This, however, is far from true for many flowers where the number of parts in a series may be increased, or much reduced by the fusion of parts, or the loss of one or more parts from any series.

The following examples will illustrate these points: *Viola* has five sepals, five petals, five stamens, three carpels; the pea has five sepals, five petals, ten stamens, one carpel; mustard has four sepals in two whorls, four petals in one whorl, six stamens in an outer whorl of two and an inner whorl of four, two sterile and two fertile carpels; many flowers have a large number of stamens in several whorls (e.g. *Rosa*). It should be noticed that owing to the abbreviation of the receptacle and other causes, it is often difficult to distinguish the separate whorls, e.g. the two whorls of sepals in mustard, the two whorls of stamens in pea.

Neglecting the reduction of parts met with in particular series, and more especially in the gynaeceum, we find that in Dicotyledons the series of floral leaves are, *as a rule*, arranged in twos, fours, or fives, or multiples of these numbers. In other words, the arrangement is *dimerous*, *tetramerous*, or *pentamerous*, rarely trimerous. The *trimerous* arrangement, *i.e.* in threes or multiples of three, is characteristic of Monocotyledons.

8. Alternation of Parts

The general rule is that the leaves of the different series alternate in position with each other—the petals alternate with the sepals, the stamens with the petals, etc. If there are several whorls of stamens, these whorls alternate with each other.

But there are exceptions. In spiral flowers, the parts are sometimes superposed. In cyclic flowers the departure from regular alternation arises from various causes. In *Primula*, for example, there are five sepals, five petals, five stamens, and the stamens are opposite to the petals (*antipetalous*). Sometimes, where there are two alternating whorls of stamens, the outer whorl is opposite the petals. This is known as the *obdiplostemonous* condition. The carpels, where fewer in number, clearly cannot alternate with the leaves of the outer series.

9. Regular and Irregular Flowers

In regular flowers the parts in each series have the same size and form, *i.e.* the sepals resemble each other, so also the petals, etc. Irregular flowers are those in which some of the floral leaves in any one series have a different shape or size from the others—for example, the petals of pea or violet.

10. Floral Symmetry

Flowers may be radially symmetrical (actinomorphic), isobilateral (zygomorphic), or asymmetrical. The planes of symmetry may be median or antero-posterior, diagonal, or lateral (see Figs. 194 and 195). Zygomorphy is frequently due to irregularity, and this is the sense in which the term is used as a rule in descriptive botany. In zygomorphic flowers the plane of symmetry is, in most cases, antero-posterior or median, *i.e.* it is the plane passing through the anterior and posterior sides of the flower, e.g. pea, violet (Figs. 195, A and B). Asymmetrical flowers are usually spiral, as for example in the Cactaceae.

11. The Receptacle: Insertion of Floral Leaves

The receptacle is nearly always short. Only occasionally is it elongated between the whorls of floral leaves, as in some species of campion (*Silene*, Fig. 174, A). The form of the receptacle varies considerably. It may be convex and more or less dilated, or flattened, or hollow and cup-shaped. The insertion of floral leaves varies according to the form of the receptacle.

In many flowers (e.g. *Ranunculus*, *Silene*, *Papaver*) the receptacle is more or less convex. The gynaeceum is developed at the apex of the receptacle; the stamens, petals, and sepals, are inserted, *in order*, on the side of the receptacle below the gynaeceum. This is the **hypogynous** arrangement (Fig. 174, A).

Suppose now that the receptacle is not convex, but forms a flattened circular disc. The apex of the receptacle is, of course, in the middle of the disc, and the flattened form is due to the sides of the receptacle having grown up to the same level. The gynaeceum is developed in the middle of the disc, and the sepals, petals, and stamens round the rim or margin. They are not *underneath* the gynaeceum, but *round about* it. Hence this is called a **perigynous** arrangement (Fig. 174, C). Sometimes the carpels are borne on a conical protuberance in the middle of the disc; this would represent

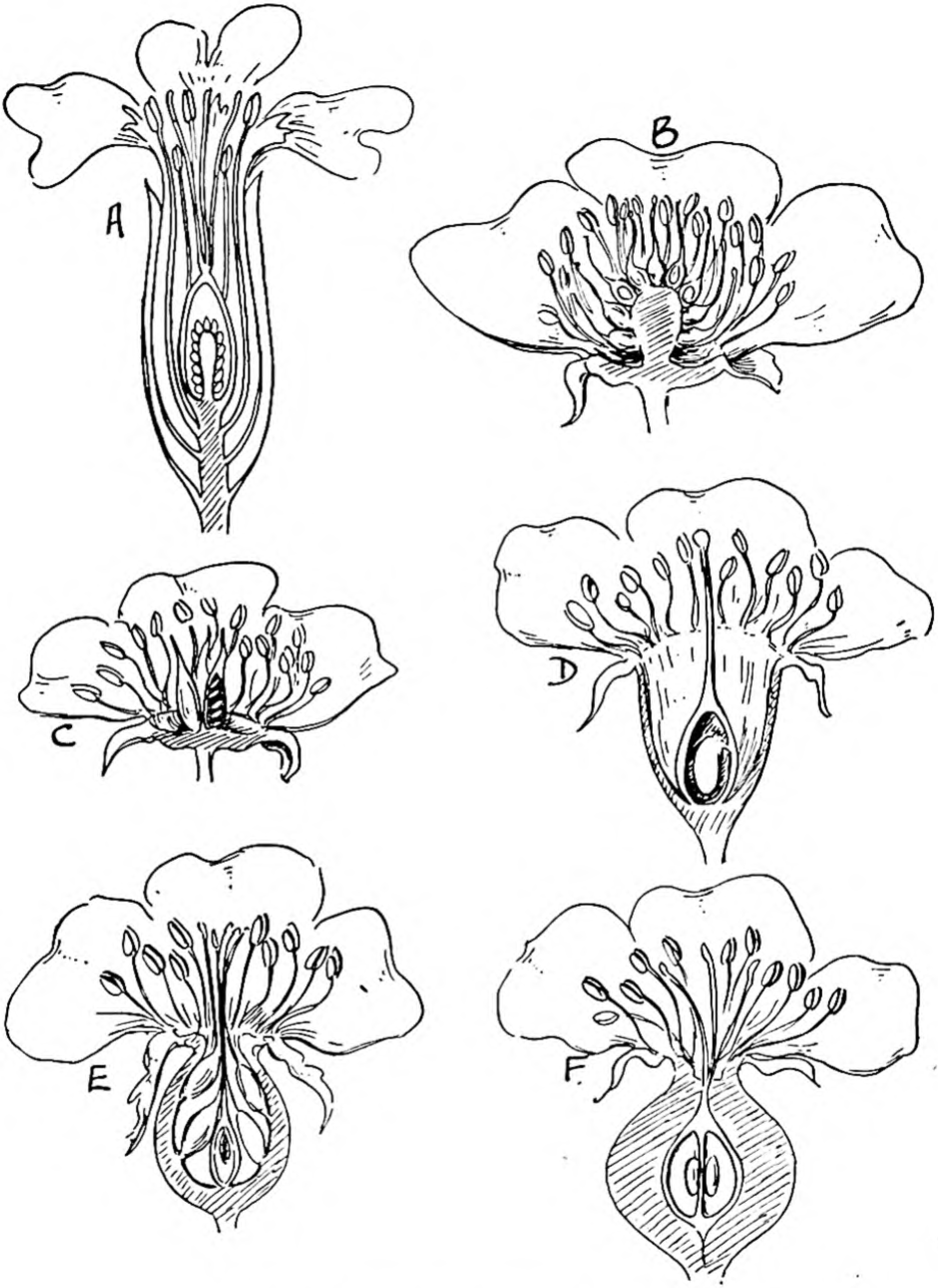


Fig. 174. Types of Floral Receptacle.

Longitudinal sections (half-flowers) of

A, *Silene*; B, *Rubus*; C, *Filipendula*; D, *Prunus*; E, *Rosa*; F, *Pyrus*.

a continued growth of the apex (e.g. *Fragaria, Rubus,* etc., Fig. 174, B).

It is with the perigynous condition that the student will experience most difficulty; there are so many degrees of it. The receptacle may not be flat, but hollowed out, and more or less cup-like. This is due to the sides of the receptacle continuing to grow above the apex, which lies at the bottom of the cup (Fig. 174, D). The carpels (gynaeceum) are developed in the cup; the sepals, petals, and stamens from the rim of the cup. This also is a perigynous condition. A still more extreme form of perigyny is found in wild rose (Fig. 174, E). Here there is a very deep cup.

Finally, in the **epigynous** condition (Fig. 174, F) the receptacle forms a deep cup as in the extreme forms of perigyny; but the carpels are from the first adherent to the receptacle, which is for this reason considered as part of the ovary. Thus in epigynous flowers the sepals, petals, and stamens are inserted *on* the gynaeceum. In the perigynous condition the receptacle wall remains distinct from the ovary.

12. Nectaries

The receptacle frequently bears a fleshy or glandular outgrowth, such as is found on the top of the inferior ovary in Umbelliferae and in the ivy (*Hedera*). This is termed the disc. In *Rubus* the disc lines the outer concave part of the receptacle. Usually the disc is lobed (vine), and frequently it secretes nectar. Nectaries may, however, develop from, or upon, any part of the flower. Thus in *Viola* the outgrowths borne by two stamens secrete nectar into a hollow spur borne by the anterior petal. In buttercup a small scale at the base of each of the petals covers a pocket-shaped nectary, while in christmas rose there are hollow tubular nectaries between the andrœcium and perianth. Nectaries occur upon the gynaeceum of *Gentiana*, and each sepal of *Althaea* bears a nectary on its inner surface.

13. The Calyx

The calyx may consist of numerous sepals showing a primitive spiral arrangement, as in cactus and water lily; but usually it consists of from two to five sepals. If the sepals are free, the calyx is **polysepalous.** When they are united laterally, however slightly, the calyx is **gamosepalous.** The gamosepalous condition is due, not to the actual fusion of originally separate sepals, but to common basal growth during development. In all hypogynous and perigynous arrangements the calyx is described as *inferior*; in the epigynous flower the calyx is described as *superior*.

In some flowers, e.g. *Fragaria* (strawberry), the sepals are stipulate. The stipules fuse in pairs between the sepals and produce an outer series of small sepal-like structures, forming what appears like an outer calyx. This is known as the **epicalyx** (Fig. 175).

An epicalyx may also be produced by the aggregation of bracts or bracteoles beneath the calyx, e.g. Malvaceae.

The calyx usually has a protective function. It commonly serves to protect the parts of the young flower in the bud. When the flower opens the calyx may fall off, e.g. in poppy, in which case it is said to be *caducous*, or the sepals fold back as in the wild rose. The calyx is *deciduous* if it falls off when the flower withers. But frequently it *persists* till fruiting takes place and protects the young fruit, which is developed from the ovary of the flower (e.g. strawberry and Labiatae). A gamosepalous calyx not only affords a more efficient protection to the flower-bud than a polysepalous one, but also gives support and protection to the base of the adult flower and to the developing fruit. Hence a gamosepalous calyx is never caducous.

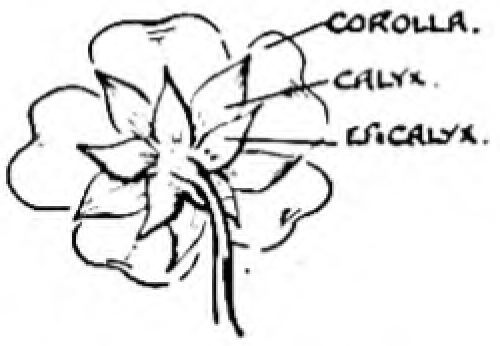


Fig. 175.
EPICALYX, CALYX AND COROLLA OF STRAWBERRY.

In Umbelliferae, where the flowers are closely aggregated, and in many Compositae, where in addition they are surrounded by a ring of bracts, a protective calyx is not required and is either very small or quite absent.

The calyx, however, may perform other functions. Thus, in many Compositae (e.g. *Taraxacum*, *Senecio*, and *Cnicus*) there is a rudimentary calyx represented by hairs, forming a silky **pappus** (Fig. 214, A), which undergoes further development after flowering, and serves to disperse the fruit. In some flowers also the sepals instead of being green, as is usually the case, are brightly coloured, and attractive. In this case the calyx is described as petaloid (Fig. 176).

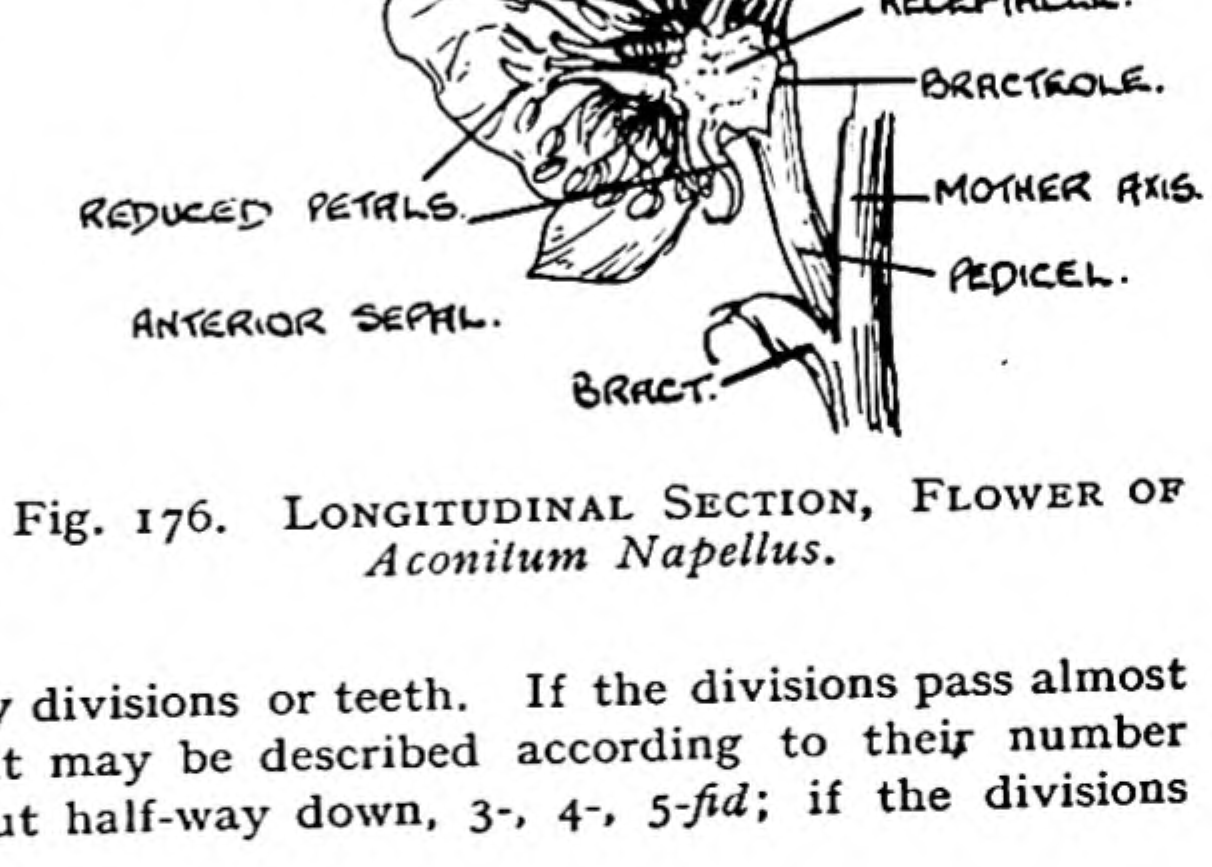


Fig. 176. LONGITUDINAL SECTION, FLOWER OF *Aconitum Napellus*.

In a polysepalous calyx the outline of the individual sepals is described in the same terms as are used for ordinary foliage leaves. The number of sepals in a gamosepalous calyx is usually indicated by divisions or teeth. If the divisions pass almost to the base of the calyx, it may be described according to their number as 3-, 4-, 5-*partite*; if about half-way down, 3-, 4-, 5-*fid*; if the divisions are small, 3-, 4-, 5-*toothed*.

14. The Corolla

The corolla may consist of spirally arranged, free, non-coherent petals, e.g. Cactaceae; or of a single whorl (*Digitalis*, *Malva*) or, more rarely, a double whorl of petals (*Papaver*). In water lily the petals are arranged in a close spiral.

The corolla may be *polypetalous* or *gamopetalous* (cf. calyx), *regular* or *irregular*, and, as it to a large extent determines the symmetry of the flower, the terms *zygomorphic*, *actinomorphic*, are applied to it. According to the insertion of petals the corolla is described as hypogynous, perigynous, or epigynous.

The corolla serves, in most cases to attract insects to the flower in connexion with the process of pollination. It also protects the stamens and carpels, especially when the petals are united in the form of a tube enclosing these essential organs. The tube also serves as a receptacle for nectar. After fertilisation the seeds begin to develop, and the corolla is usually shed. The withered corolla, however, may persist in a few cases.

The petals are usually brightly coloured, but sometimes green (sepaloid). They may be absent, e.g. *Alchemilla* and some Ranunculaceae (*Clematis*, *Anemone*), or represented by nectar-secreting structures, e.g. *Aconitum* (Fig. 176) and *Helleborus*.

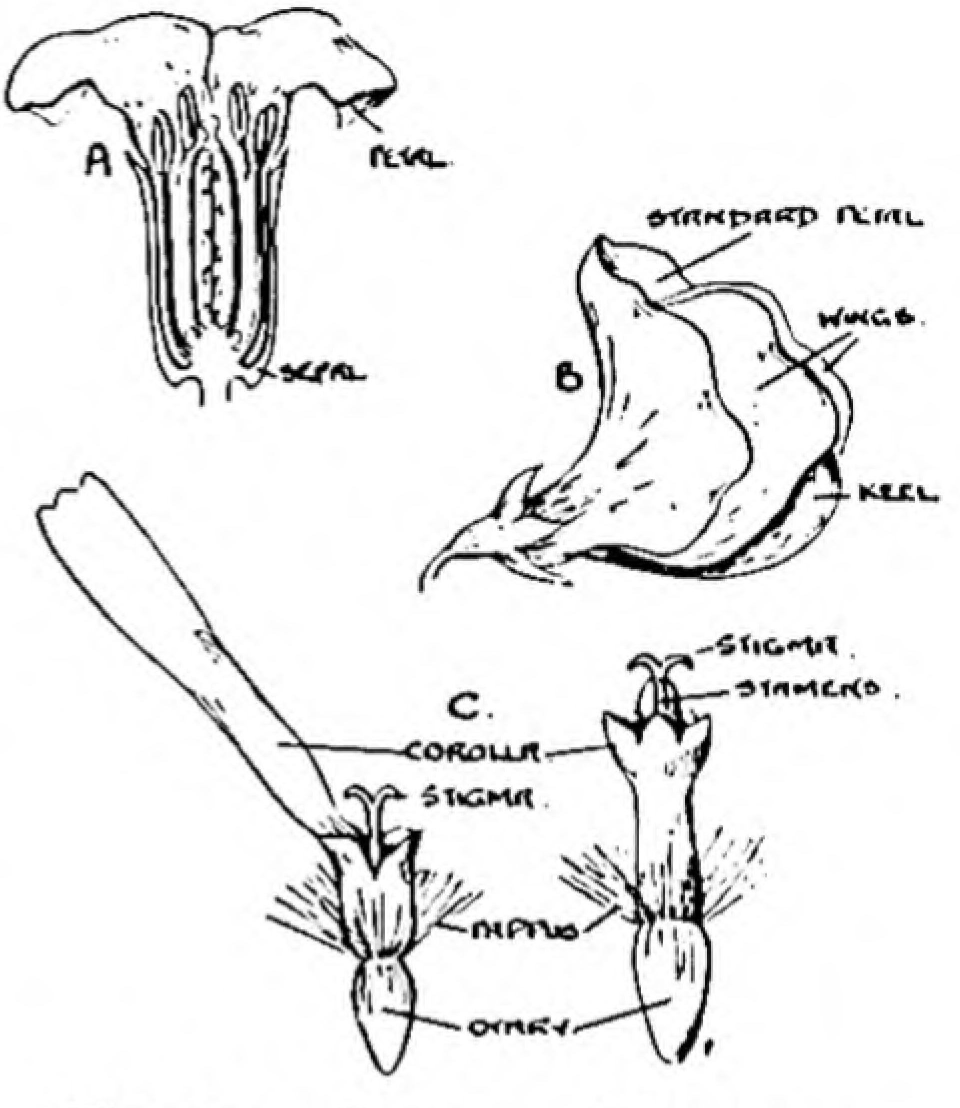


Fig. 177. FORMS OF FLOWERS.

A, *Cheiranthus* (Cruciferae), longitudinal section; B, *Lathyrus* (Papilionatae), external; C, Ligulate and tubular florets of *Aster* (Compositae).

In a polypetalous corolla the outlines of the individual petals are described in the same terms as are used for the foliage leaf, and, as in the calyx, the gamopetalous corolla may be described as 3-, 4-, 5-partite, -fid, or -toothed.

The following special terms are applied to polypetalous corollas:—*Cruciform* where the corolla consists of four clawed petals arranged crosswise, *i.e.* in the diagonal planes of the flower (e.g. mustard and Cruciferae generally, see Fig. 177, A); *rosaceous* (Fig. 174 B–E), if it consists of five spreading petals, not clawed, and attached perigynously (Rosaceae); *caryophyllaceous* (Fig. 174, A), if it consists of five clawed petals, with spreading limbs attached hypogynously to the receptacle inside a slender tubular calyx (pinks and many Caryophyllaceae); *papilionaceous* (from the supposed resemblance to a butterfly), if it consists of five petals, one large—the standard, two lateral—wings, and two fused to form a boat-shaped structure—the keel, e.g. pea and other members of the Papilionatae (Leguminosae, Fig. 177, B).

15. The Perianth

A perianth, when not distinguished into calyx and corolla, is described in much the same way; but the terms *polyphyllous* and *gamophyllous* are used to indicate the free and coherent condition, respectively, of the perianth leaves.

16. The Corona

This is the term applied to the whole series of outgrowths developed on the corolla or perianth of certain flowers. In *Narcissus*, where the perianth is gamophyllous, the outgrowths are coherent, and the corona is cup-shaped (Fig. 227).

17. Aestivation

This has already been referred to (see p. 136). The aestivation of the perianth (or calyx and corolla) only can be studied. The folding of the individual floral leaves is described in the same terms as are used for foliage leaves. The aestivation of calyx or corolla (Fig. 111) may be *valvate*, *imbricate*, or *contorted* (*twisted*). Aestivation may be recognised either by taking transverse sections of young flower-buds, or carefully removing the young floral leaves one after the other.

18. The Androecium

A stamen (Fig. 178) consists of three parts—**filament, anther,** and **connective.** The morphology of the stamen is discussed in Chapter XVII. The anther is usually two *lobed*, and contains **microspores** or **pollen-grains.** These lie in four cavities, the **microsporangia** or **pollen-sacs** (Fig. 179), of which there are two in each anther-lobe.

The anther-lobes are connected by a strip of tissue containing a vascular bundle. This is the *connective*. It is usually narrow, and the anther-lobes lie close together, but may be elongated so that the lobes are widely separated, as in some Labiatae.

In a few cases (e.g. *Malva*, *Corylus*, *Carpinus*) the stamens when quite young undergo division or segmentation, and thus in the fully developed flower the anthers have only one anther-lobe with two pollen-sacs.

Sometimes special appendages are developed on stamens. These generally arise as outgrowths of the connective. In *Viola* there is a membranous orange-coloured outgrowth on top of each anther, and, in addition, the two antero-lateral stamens have each a green elongated process (functioning as a nectar gland) passing down into the spur of the anterior petal (Figs. 209 and 268).

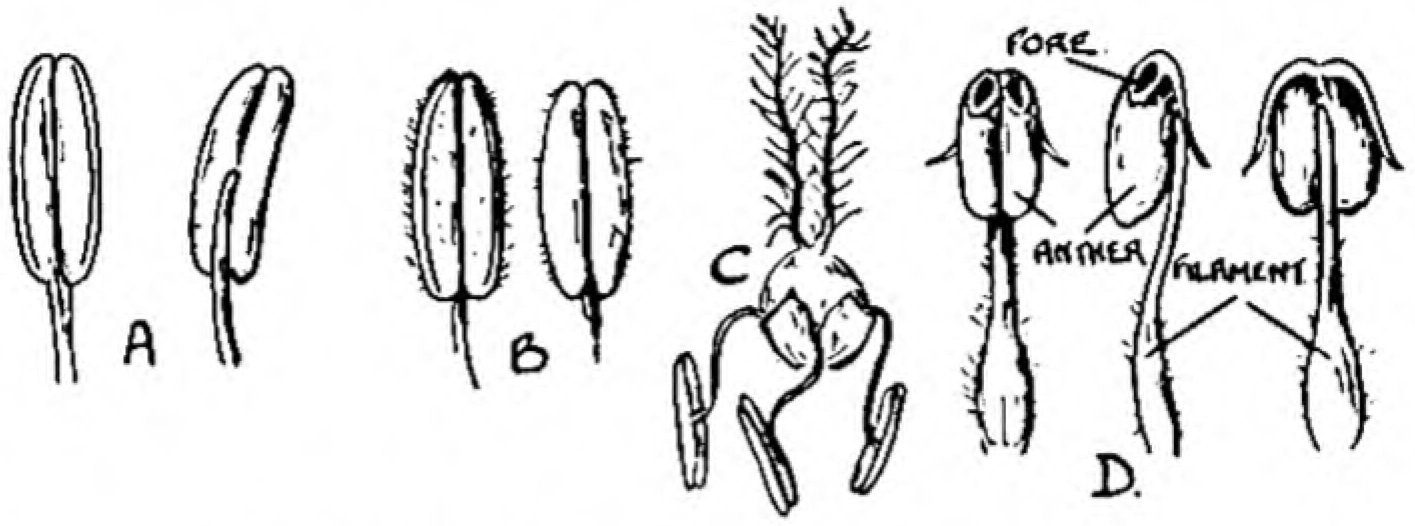


Fig. 178. STAMENS, EXTERNAL VIEW.
A, Adnate, dorsifixed (*Nicotiana*); B, Innate, basifixed (*Datura*);
C, Versatile, dorsifixed (*Triticum*); D, Poricidal dehiscence (*Arctostaphylos*).

Barren or rudimentary stamens are called **staminodes.** They may consist only of filament or be represented by various modified forms.

Some genera such as *Rosa* and *Prunus* which have "single" flowers in the wild state, possess "double" flowers in cultivated forms. If such "double" flowers are dissected it is frequently possible to trace a transition from stamens, and often from carpels also, to petals. Where doubling is complete the flower is sterile and such horticultural varieties are propagated vegetatively.

The stamens may be hypogynous, perigynous, or epigynous; but sometimes, owing to common basal growth, they adhere to the corolla (or perianth). They appear then to be developed on the petals, and are said to be **epipetalous** (*epiphyllous*, if on a perianth). This is found in many gamopetalous, or gamophyllous, orders of Angiosperms, e.g. Compositae, Labiatae, Convolvulaceae. Sometimes the stamens are adherent to the gynaeceum, e.g. in orchids; this is the *gynandrous* condition.

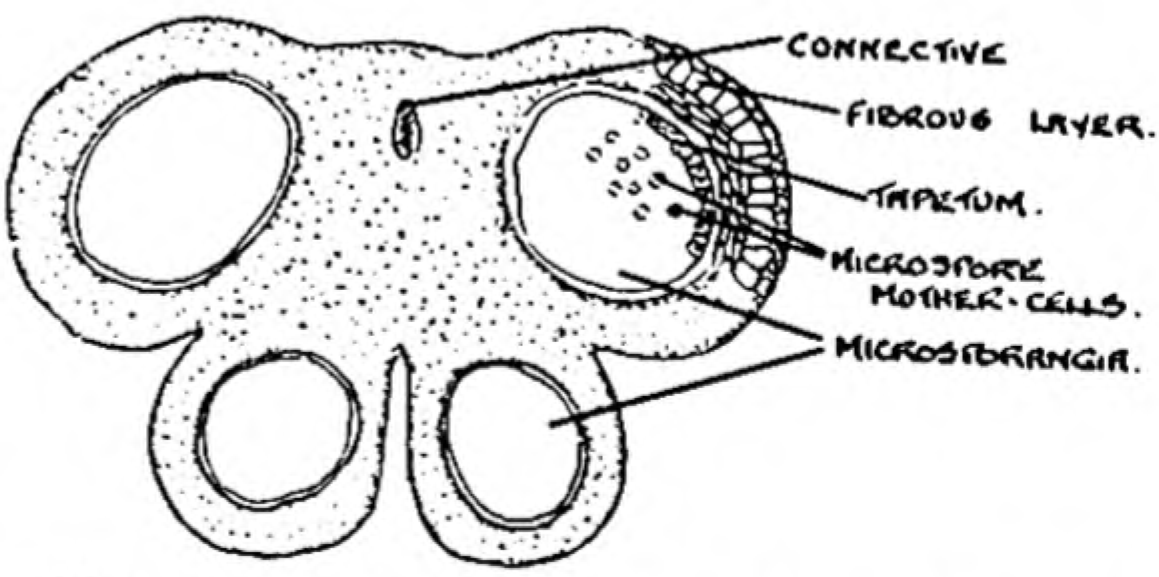


Fig. 179. TRANSVERSE SECTION, YOUNG UNDEHISCED ANTHER OF *Lilium*.

If the stamens are free from each other, *i.e.* not coherent, the androecium is **polyandrous** (diandrous, triandrous, pentandrous, etc., according to the number). If united, the union may be of two kinds. (*a*) The stamens cohere by their filaments: this is the **adelphous** condition—**monadelphous** if all are united to form a tube round the pistil, **diadelphous** if united in two groups, *polyadelphous* if in several groups. The monadelphous condition is found, for example, in *Malva* and some Papilionatae; the diadelphous, in other Papilionatae (e.g. pea) where, of the ten stamens, nine are fused and the tenth is free; the polyadelphous, in Anonaceae and Rutaceae. (*b*) The stamens cohere by their anthers, the filaments being free. This is characteristic of Compositae, some Solanaceae (e.g. *Solanum* species), etc. It is the **syngenesious** condition.

Where the stamens in a flower have different lengths, special terms are sometimes applied to the androecium. Thus, in the Family Cruciferae, there are frequently four long and two short stamens (Fig. 177, A), and the androecium is said to be **tetradynamous.** In Labiatae (e.g. Fig. 274) and Scrophulariaceae (e.g. Fig. 278), where there are two long and two short stamens, it is **didynamous.** These are the only common orders in which these terms are used.

19. Insertion of the Anthers

The attachment of the anther to the filament should be noticed (Fig. 178). It is *innate* or *basifixed* if the anther is fixed directly on top of the filament; *adnate* if the connective is well marked, and there is no articulation of the filament to the base of the anther, so that the filament seems to run up the back of the anther; *dorsifixed* if the filament is attached to the back of the anther and the anther is immovable; *versatile* if the attachment is similar, but the anther swings on the filament.

20. Development of Stamen

The stamen arises as a protuberance on the receptacle, and soon shows an external differentiation into anther and filament. At an early stage in the development of the anther, the two anther lobes appear. Further development can be followed by means of sections of progressively older material, which has been carefully fixed and stained, viewed under a microscope.

21. Development of the Anther (Fig. 180)

In each anther-lobe two groups of hypodermal cells divide by periclinal walls, separating an outer layer of cells from an inner. The latter is the **primary archesporium.** The cells of the outer layer further divide by two successive periclinal walls to form three layers of cells. The outermost of these layers becomes the *fibrous layer* of the anther wall, and the innermost becomes the *tapetum*. The primary archesporium divides repeatedly to form ultimately the **spore-mother cells.** Each spore-mother cell, by tetrad division, gives rise to four *microspores* or pollen-grains. The process of nuclear division of the spore-mother cell to form four daughter cells is known as **reduction division** or **meiosis.**

We have already seen that mitosis involves the resolving of the cell nucleus into a number of chromosomes. Each chromosome splits longitudinally and the halves separate and move to opposite poles, where they associate together as two daughter nuclei. Thus in mitosis the daughter nucleus has the same number of chromosomes as the parent nucleus.

In meiosis, on the other hand, each daughter nucleus has only half the number of chromosomes of the parent nucleus. The reason for this is that at the first division of the spore-mother-cell nucleus, whole chromosomes move to opposite poles. This division is quickly followed by a second division corresponding to ordinary mitosis. These two divisions constitute the process of meiosis.

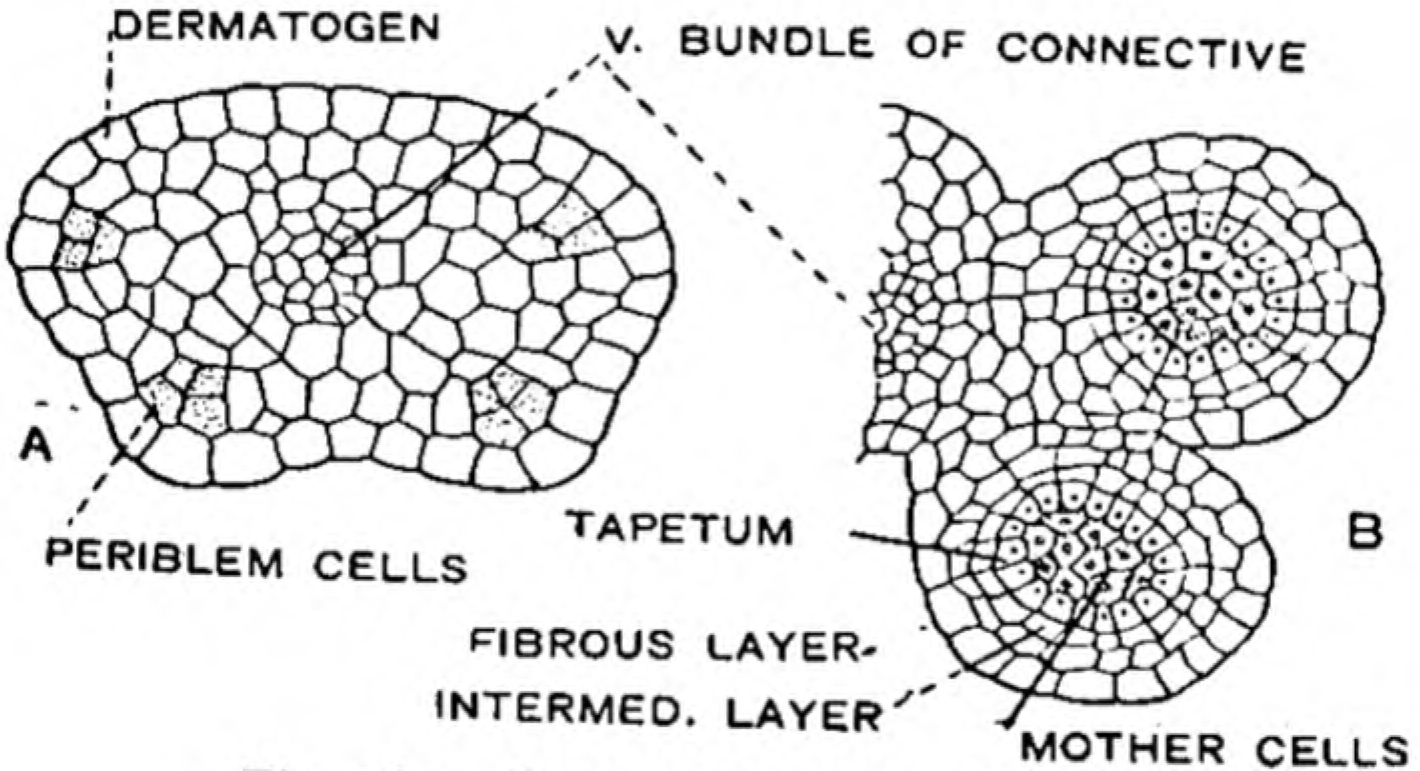


Fig. 180. DEVELOPMENT OF ANTHER.

The behaviour of the nucleus during meiosis is as follows. The spore-mother-cell nucleus resolves itself into distinct slender threads, the chromosomes. These associate in pairs, but not at random, because it has been shown that one chromosome of each pair comes from the male, the other from the female parent of the preceding generation. The partners of each pair of chromosomes are thus said to be homologous. Such a pair of chromosomes (*a* and *b*) is represented diagrammatically in Fig. 181 (I), and their behaviour subsequently traced. They tend to shorten, thicken, and intertwine (II), and at this stage, if not before, it is quite clear that each partner of the pair is split longitudinally into two except at the centromere. The two halves of each chromosome are called **chromatids** (numbered 1, 2, 3, and 4 in the diagram). The paired chromosomes lie at the nuclear (equatorial) plate of the mother cell (Prophase). The partners of each pair tend to fall apart somewhat, but still maintain intimate contact in one or more regions along their length (Metaphase). One of these points of contact is the **centromere.** Corresponding with other points of contact we may get a transverse division of two chromatids, one of each pair of chromosomes, as in II, 1 and 3. These transverse divisions divide the chromatids into segments of corresponding length, and the points at which they occur are the **chiasmata.** From the centromere, forces operate which bring about the complete separation of the two chromosomes, except that in the process of being forced or pulled apart similar segments of two chromatids of the homologous pair of chromosomes may change places. Thus, in II, III, and IV, the segment at the upper end of chromatid 3 changes place with the corresponding segment from chromatid 1. This process is called **crossing over.** It involves an interchange of nuclear material between two chromatids of an homologous pair of chromosomes.

The separated chromosomes (*a* and *b*) continue to move along a spindle which has meanwhile been forming, to opposite poles of the cell (Anaphase). If crossing over has taken place, these chromosomes are not exactly identical with those which entered into association at the beginning (compare Fig. 181, I, *a* and *b*, with IV, *a* and *b*). This has an important bearing on genetics.

Usually no cell-wall is formed at this stage between the two sets of chromosomes thus separated (Telophase), and the second division follows immediately. In this division the chromatids separate, 1 from 2, 3 from 4. The result is four daughter nuclei, each of which has only half the chromosome complement of the original mother nucleus of the spore-mother-cell. Each of these four nuclei is said to be haploid. This condition is conveniently represented by the symbol n, and the diploid condition by $2n$.

The spore-mother-cell nucleus has now given rise to four daughter nuclei. Each of these becomes associated with cytoplasm, and around each cytoplasmic mass is secreted a cell-wall. The nutritive material for this development, which also involves expenditure of energy, is supplied by the tapetum. The four cells thus formed may remain associated together in tetrads, frequently forming regular geometrical figures such as triangular pyramids, but more usually they separate as individual microspores. Meanwhile the anther has been growing, and the microspores occupy the four cavities in most mature anthers. Simultaneously the anther wall develops and some differentiation takes place in it in relation to a dehiscence mechanism. This may take the form of a fibrous layer, immediately below the epidermis, the cells of which have characteristically thickened walls (Fig. 182).

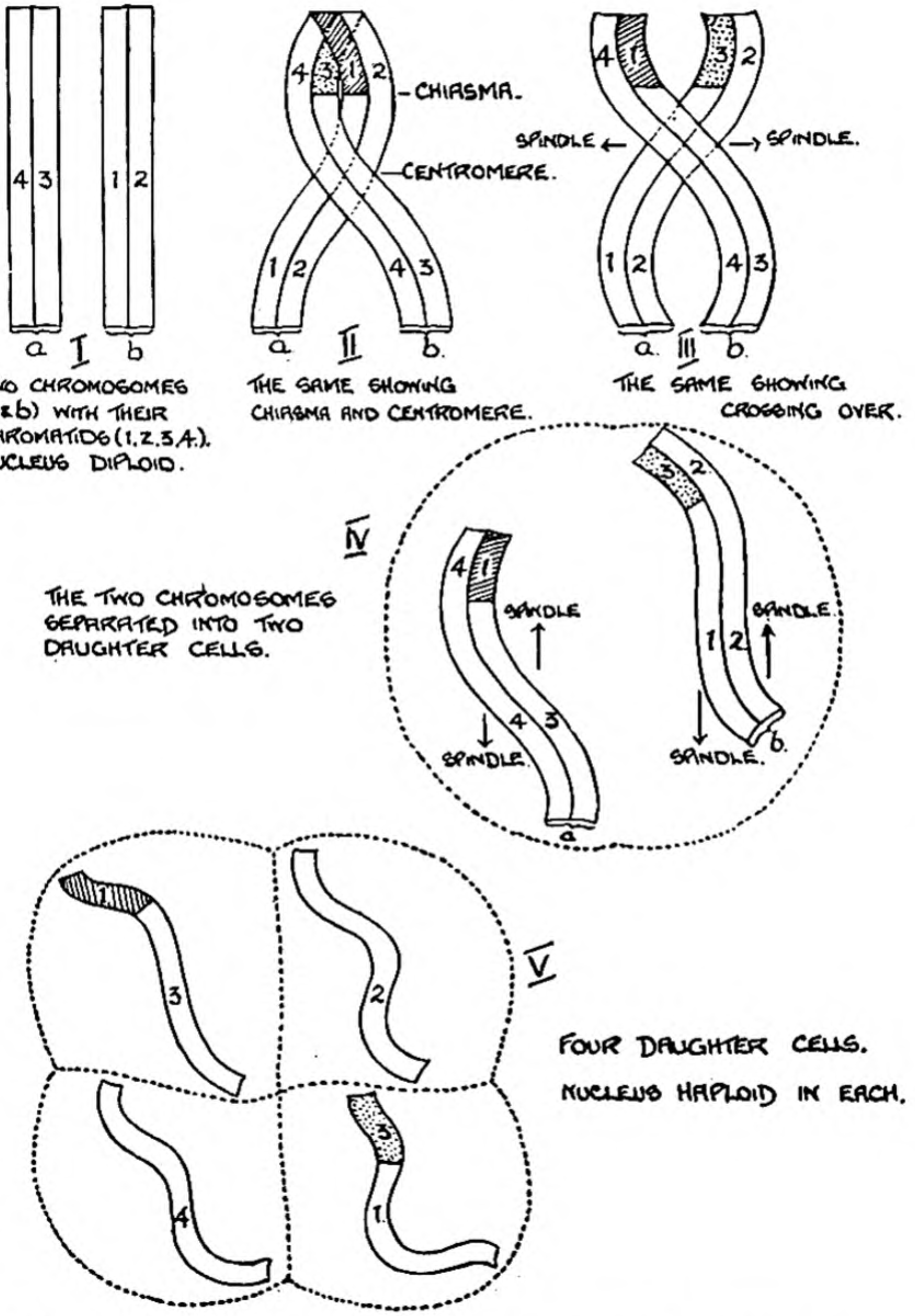
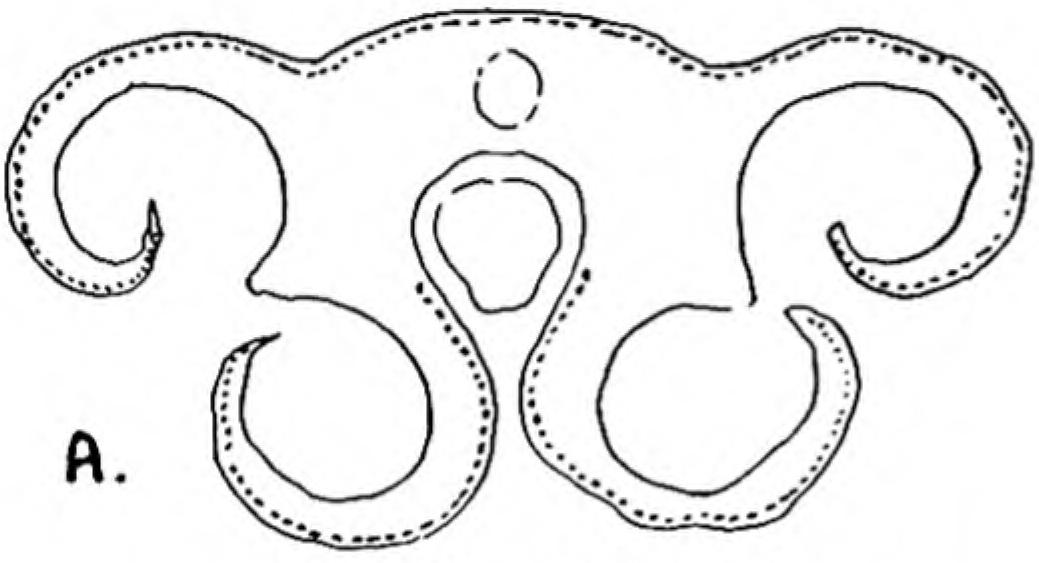

4 3
1 2
a I b
TWO CHROMOSOMES (a&b) WITH THEIR CHROMATIDS (1.2.3.4.). NUCLEUS DIPLOID.
4 3 1 2
CHIASMA.
CENTROMERE.
1 2 4 3
a II b.
THE SAME SHOWING CHIASMA AND CENTROMERE.
4 1 3 2
SPINDLE
SPINDLE.
1 2 4 3
a. III b.
THE SAME SHOWING CROSSING OVER.
IV
THE TWO CHROMOSOMES SEPARATED INTO TWO DAUGHTER CELLS.
4 1
SPINDLE
4 3
SPINDLE.
a
3 2
SPINDLE.
1 2
SPINDLE.
b.
V
1 3
2
4
3 1
FOUR DAUGHTER CELLS.
NUCLEUS HAPLOID IN EACH.

Fig. 181. DIAGRAM ILLUSTRATING MEIOSIS AND CROSSING OVER.

22. Dehiscence of the Anther

In order that the microspores may be liberated to bring about pollination, the anther dehisces. When this takes place in many stamens a longitudinal split appears between each pair of pollen-sacs in each anther lobe. This split gradually enlarges by the separation and curling back of the anther wall on either side of it (Fig. 182). The wall separating the two pollen-sacs also breaks down, and thus the pollen-sacs are exposed as one cavity. Two such cavities will therefore be formed in each anther, one on either side of the connective. If these cavities face towards the centre of the flower, the dehiscence is said to be *introrse*; if towards the outside, *extrorse*; if sideways, *lateral*.



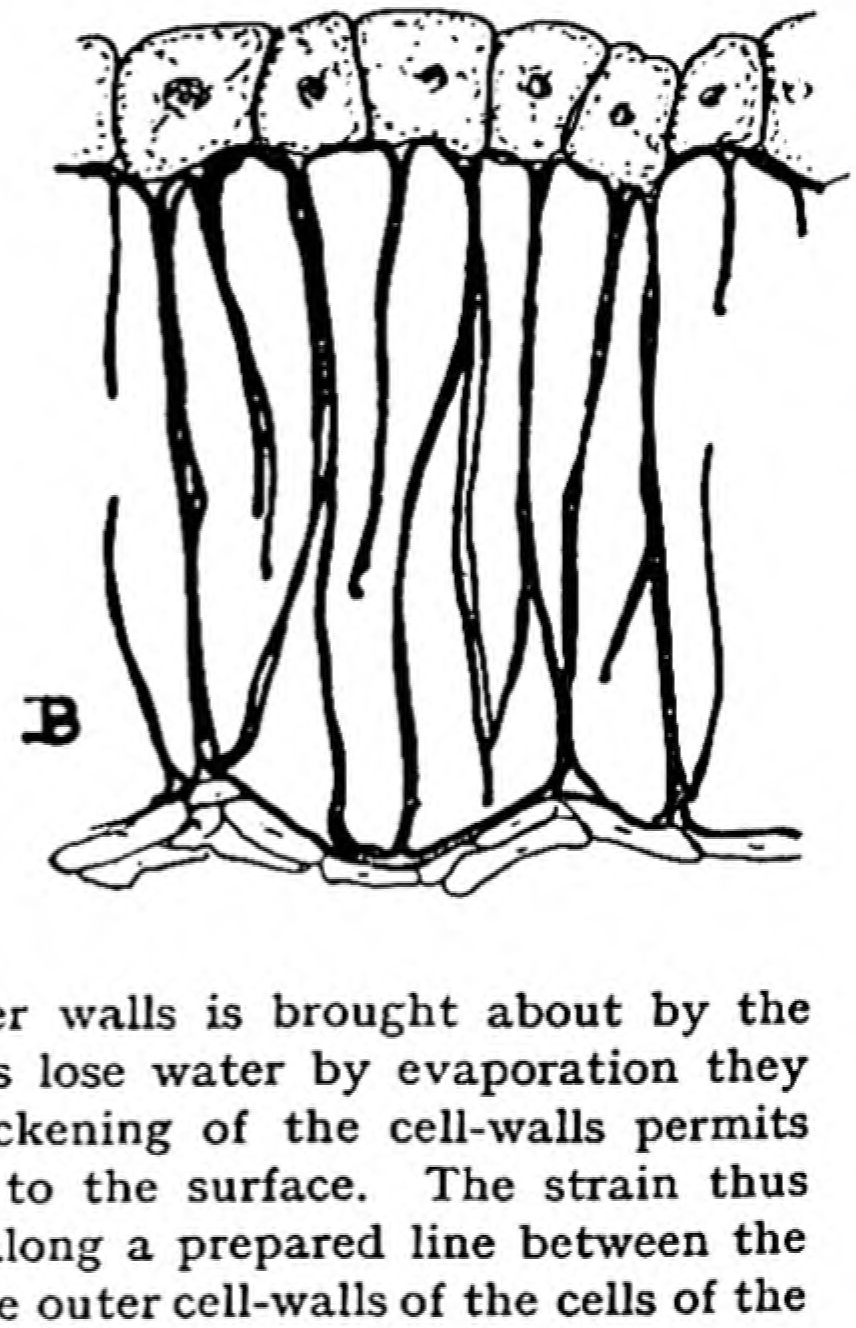


Fig. 182.

A, Dehisced Anther, Transverse Section (Diagrammatic).
B, One cell of fibrous layer much enlarged to show detail of thickening of anticlinal walls.

The splitting and curling of the anther walls is brought about by the action of the fibrous layer. As these cells lose water by evaporation they contract, but the arrangement of the thickening of the cell-walls permits of contraction only in the plane parallel to the surface. The strain thus set up causes a break in the anther wall along a prepared line between the pair of pollen-sacs in each anther lobe. The outer cell-walls of the cells of the fibrous layer contract at a much greater rate than the inner walls on account of the differential thickening. Hence the curling outwards and backwards of the anther walls. (See Chap. IX, Movements of Non-living Tissues, p. 228.)

The microspores vary much in size, form and colour, in different plants. At first they are unicellular and the wall consists of two membranes. The outer coat, the *exine*, frequently has protuberances, spines, etc., and also one or more areas where the wall is thin and forms a pore. The inner coat, the *intine*, is thin and consists of cellulose. In some plants, e.g. orchids, the microspores are not loose, but those of each anther lobe are aggregated into a single mass called a **pollinium** (Fig. 183).

Before seed can be produced the microspores must be transferred to the stigma, either of the same flower, or of another flower of the same species; a process called pollination.

23. The Gynaeceum or Pistil

The gynaeceum or pistil consisting of **megasporophylls** or **carpels** forms the inner essential organ of the flower. It may consist of one or of several carpels. In the latter case, according to the number, it is bicarpellary, tricarpellary, etc.

The morphology of the carpel is discussed in Chapter XVII. The old classical view represents it as a single carpellary leaf folded with the lower side outermost and its margins coherent along a line (*the ventral suture*), and, further, with the apex of the leaf elongated and slightly swollen at the tip.

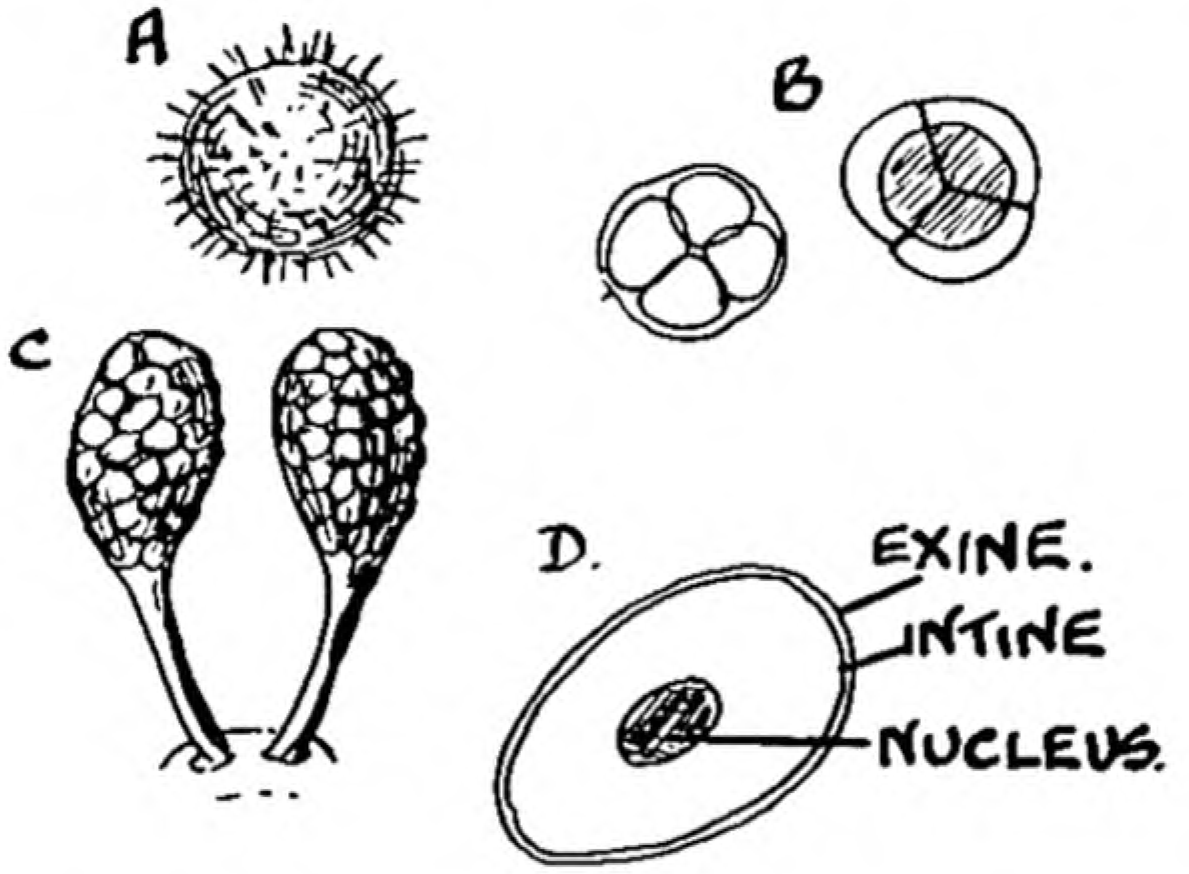


Fig. 183. TYPES OF MICROSPORES.
A, *Althaea*: B, *Arctostaphylos* (tetrads): C, *Orchis* (pollinia); D, Optical section of a microspore.

In such a **monocarpellary pistil** (Fig. 184) the hollow basal portion of the folded carpel is the **ovary**, from which the fruit is afterwards developed; it contains a varying number of ovoid or rounded bodies, the **ovules** or **megasporangia**, which after fertilisation develop into seeds. The slender prolongation, of varying length, on top of the ovary is the **style**, which usually contains a central cavity communicating with the cavity of the ovary, but may be composed of loose tissue throughout. The apical portion of the style, called the **stigma**, is usually swollen and covered with hairs or glandular papillae; as we shall see later, it forms the receptive surface for the microspores. When there is no style, the stigma is said to be sessile on the ovary.

If we examine the ovary, we find that the ovules are developed in two rows, each row on a longitudinal ridge or cushion of tissue called the **placenta,** along the ventral suture, on the inner surface of the ovary wall. The dorsal suture is opposite to it. The **placentation** (*i.e.* the position or arrangement of placentas in an ovary) in the *simple* ovary is described as marginal. The pistil of the Papilionatae (pea, bean, etc.) is a good example of this.

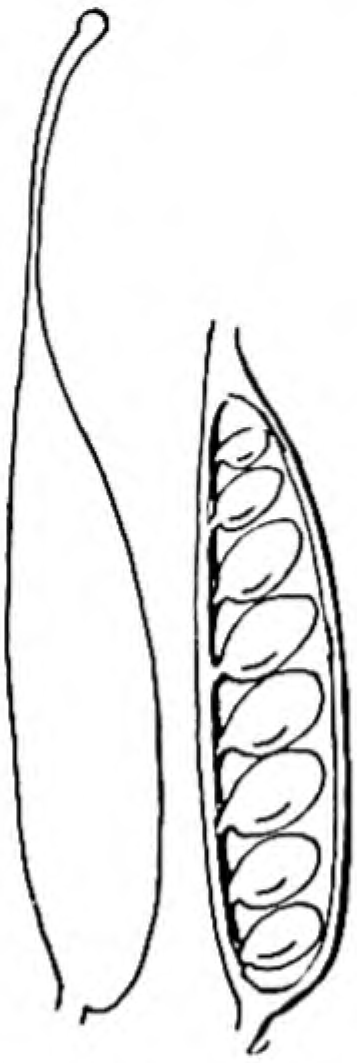


Fig. 184. MONOCARPELLARY GYNAECEUM, CARPEL OF LEGUMINOUS FLOWER.

Although morphologists have compared the formation of the monocarpellary pistil to the folding of a carpellary leaf, we must not assume that this process can be observed during the development of the flower. But in certain Gymnosperms the ovules are not enclosed in an ovary, but are borne on the open megasporophylls. In *Cycas* they are borne on the margins of the megasporophylls. They imagined such a megasporophyll folded so as to bring the margins together and form a cavity enclosing the ovules, thus giving the condition found in such Angiosperms as the pea.

24. Polycarpellary Gynaeceum

Of this there are two conditions, according as the carpels are or are not united with each other. If the carpels are free, *each* forms a simple ovary, style and stigma, like the single carpel of the monocarpellary pistil. This is the **apocarpous** condition (Fig. 172, A; 174, B, C). Here, while there is a single gynaeceum or pistil in the flower, there is a number of simple ovaries. The number indicates the number of carpels. The placentation is marginal. Frequently, only one ovule is developed in each loculus (many Ranunculaceae and Rosaceae).

In the second condition all the carpels are united to form a single *compound* ovary, and the pistil is **syncarpous.** The union may or may not be complete. If complete, the ovary bears a single style and stigma (Fig. 185, A), and it is only by the internal structure of the ovary that the number of carpels can be

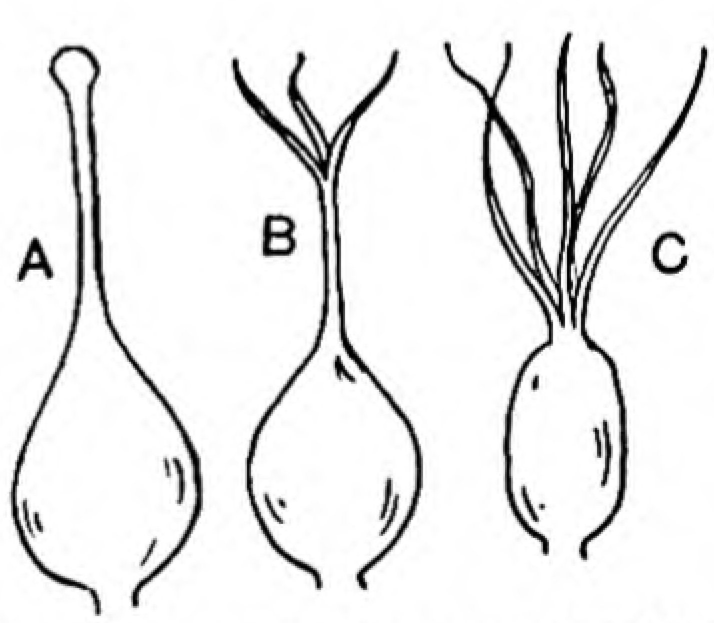


Fig. 185. DEGREES OF FUSION OF STYLE.

A, *Primula*; B, *Luzula*; C, *Stellaria*.

determined. If incomplete, a number of styles or stigmas are borne on the single ovary (Fig. 185, B, C), owing to the apices of the carpels remaining free. With few exceptions the number of styles or stigmas is the same as the number of carpels. Hence, e.g. in Compositae (Fig. 177, C), where the style is single, but there are two stigmas, we assume that the pistil is bicarpellary.

The structure of the ovary and the placentation in the syncarpous pistil differ in different cases. The following conditions should be noticed:—

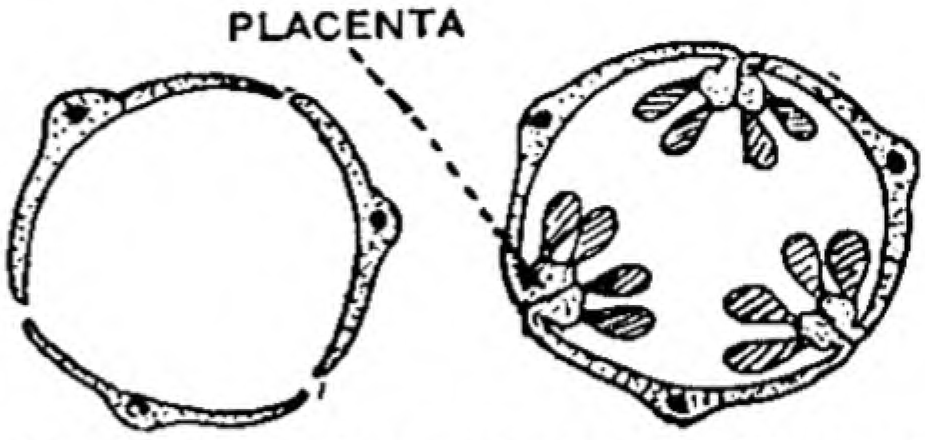


Fig. 186. DIAGRAMMATIC REPRESENTATION OF THE UNION OF THREE CARPELS TO FORM A UNILOCULAR OVARY WITH PARIETAL PLACENTATION, e.g. *Viola*, SEEN IN TRANSVERSE SECTION.

(*a*) If the carpels are fused by their adjacent margins (Fig. 186) they form a unilocular ovary. The fused margins are the placentas bearing ovules, and the placentation is marginal and parietal. The number of parietal placentas indicates the number of carpels.

(*b*) If the carpels are folded on themselves before fusing, that is, if the fused margins run in to the middle of the ovary (Fig. 187), a multilocular ovary results and the marginal placentas of all the carpels fuse in the centre to form a central or axile column. The placentation is marginal and **axile**. The number of loculi, or the number of septa by which the ovary is divided, indicates the number of carpels (except where *false* septa are formed—see below). Sometimes only one ovule is developed in each loculus (Fig. 188).

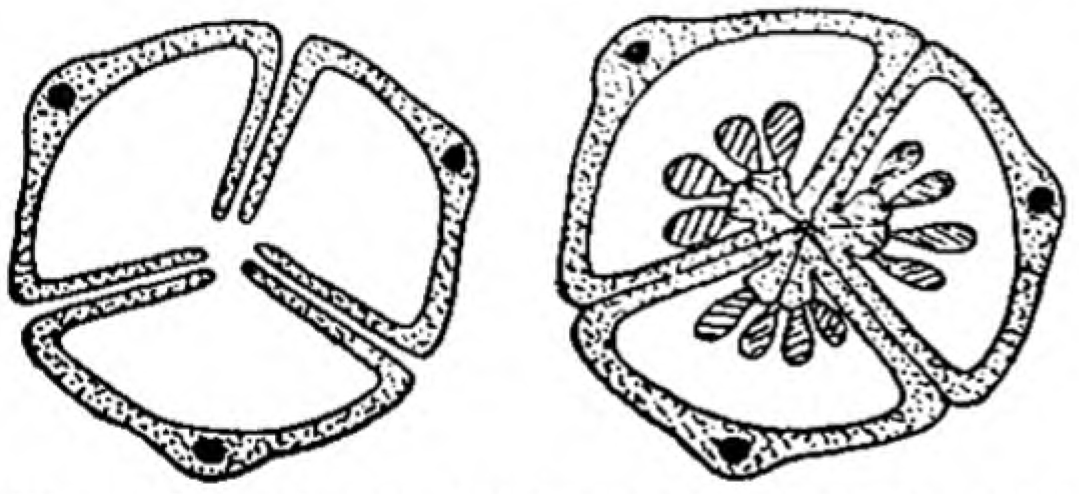


Fig. 187. DIAGRAMMATIC REPRESENTATION OF THE UNION OF THREE CARPELS TO FORM A TRILOCULAR OVARY WITH AXILE PLACENTATION, e.g. *Lilium*, SEEN IN TRANSVERSE SECTION.

In the ovary of poppy there is an intermediate condition between (*a*) and (*b*). The septa, which are covered with ovules and are therefore placentas, do not reach the middle of the ovary. The ovary is unilocular, but partially divided. The placentation is parietal.

(*c*) If the carpels fuse by their adjacent margins and the ovary is unilocular as in (*a*), and the ovules are not developed on the carpellary margins, but are borne on a central axis running through the middle of the ovary, the placentation is **free-central.** In typical cases (Myrsinaceae) the central axis is a prolongation of the receptacle into the ovary. The ovules are developed on the axis of the flower, not on the carpels. There are, however, a few families (e.g. Caryophyllaceae) in which the free-central placenta appears to be derived from an originally axile placentation by the breaking down of the septa.

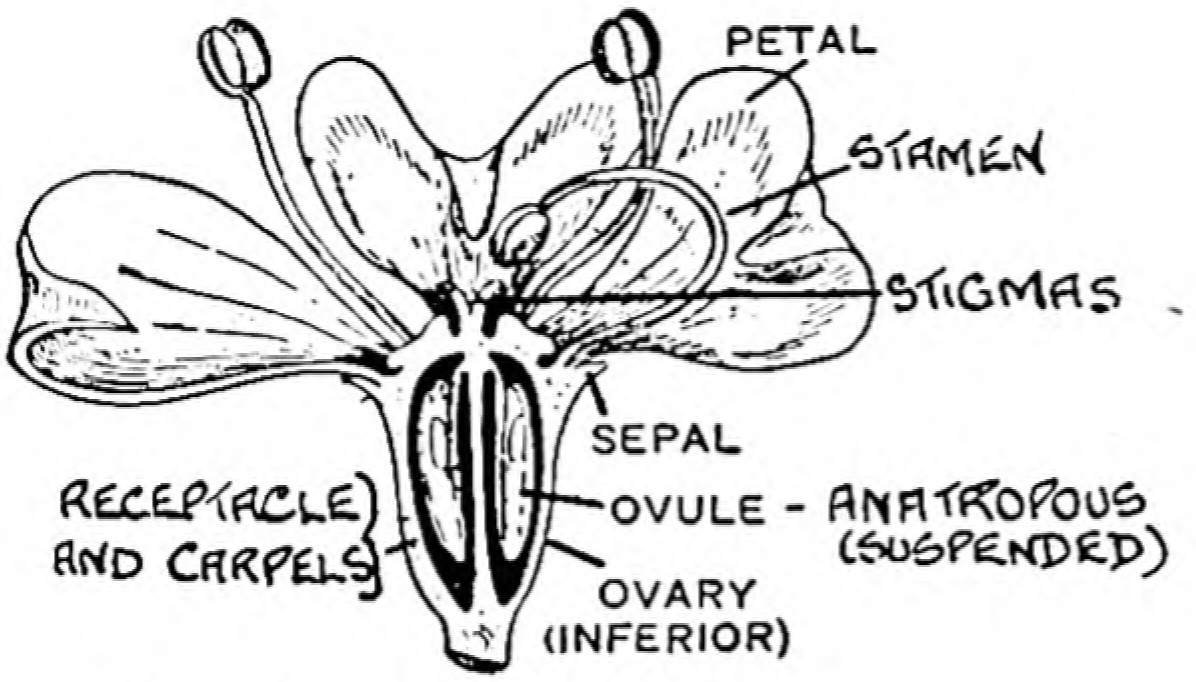

PETAL
STAMEN
STIGMAS
SEPAL
RECEPTACLE AND CARPELS
OVULE - ANATROPOUS (SUSPENDED)
OVARY (INFERIOR)

Fig. 188. FLOWER OF UMBELLIFERAE.
(Half-flower in vertical section.)

Basal placentation is a modification of typical free-central. Here a single ovule is inserted on the floor of the ovary. It is developed on the receptacle, which, however, is not prolonged as an axis into the ovary (e.g. Polygonaceae, Fig. 189, and Compositae).

The ovules are, in rare cases, developed, not on the margins of the carpels, but over the whole inner surface, e.g. the flowering rush (apocarpous) and white water lily (syncarpous). This is called **superficial placentation.**

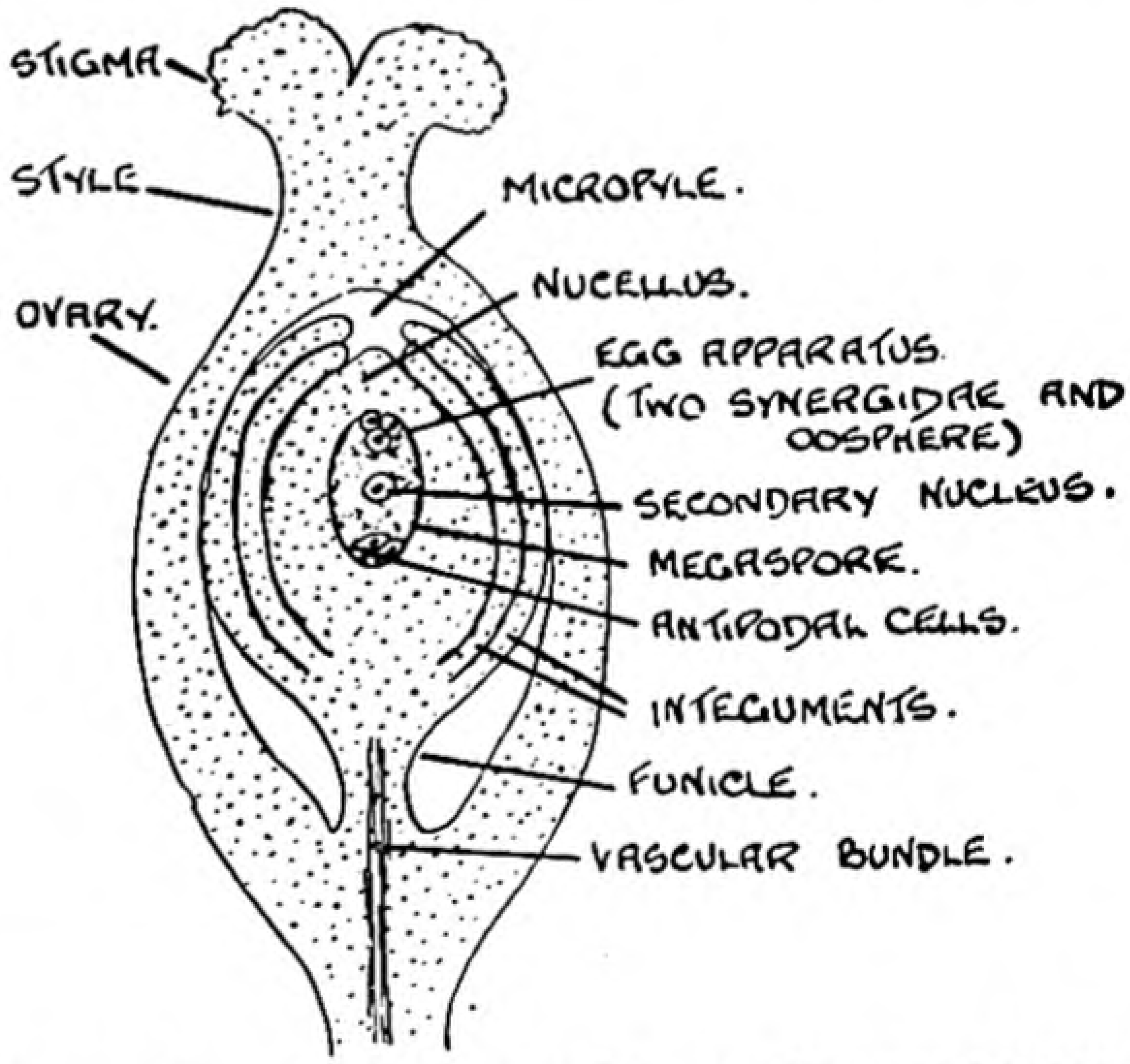

STIGMA
STYLE
OVARY
MICROPYLE.
NUCELLUS.
EGG APPARATUS (TWO SYNERGIDAE AND OOSPHERE)
SECONDARY NUCLEUS.
MEGASPORE.
ANTIPODAL CELLS.
INTEGUMENTS.
FUNICLE.
VASCULAR BUNDLE.

Fig. 189. OVARY AND BASAL ORTHOTROPOUS OVULE OF *Polygonum*.
Diagrammatic Longitudinal Section.

25. True and False Septa

True septa, or dissepiments, are those which represent the inturned margins of carpellary leaves. Septa formed in any other way, e.g. as ingrowths from the surfaces of the carpels, are *false*. In the ovary of Cruciferae (Fig. 190), for example, the false septum is formed by two membranes, which grow in from the two parietal placentas, and meet and fuse in the centre.

26. Superior and Inferior Ovaries

In all hypogynous and perigynous conditions, the ovary is described as *superior*; in the epigynous condition, as inferior. It might seem out of place to describe the ovary as superior, and the calyx inferior, in such perigynous conditions as are shown in Fig. 174, D and E. But it must be realised that the ovary here is developed at the morphological apex of the receptacle and is free from the calyx.

27. Development of the Ovule

The development of the ovule is followed by examining series of longitudinal sections of ovules at progressively older stages of development. The material must be specially fixed and stained for this purpose. Such ovaries as those of pea, lily and marsh-marigold are useful material for examination, and if cut transversely at different stages of development the sections will show ovules cut more or less longitudinally.

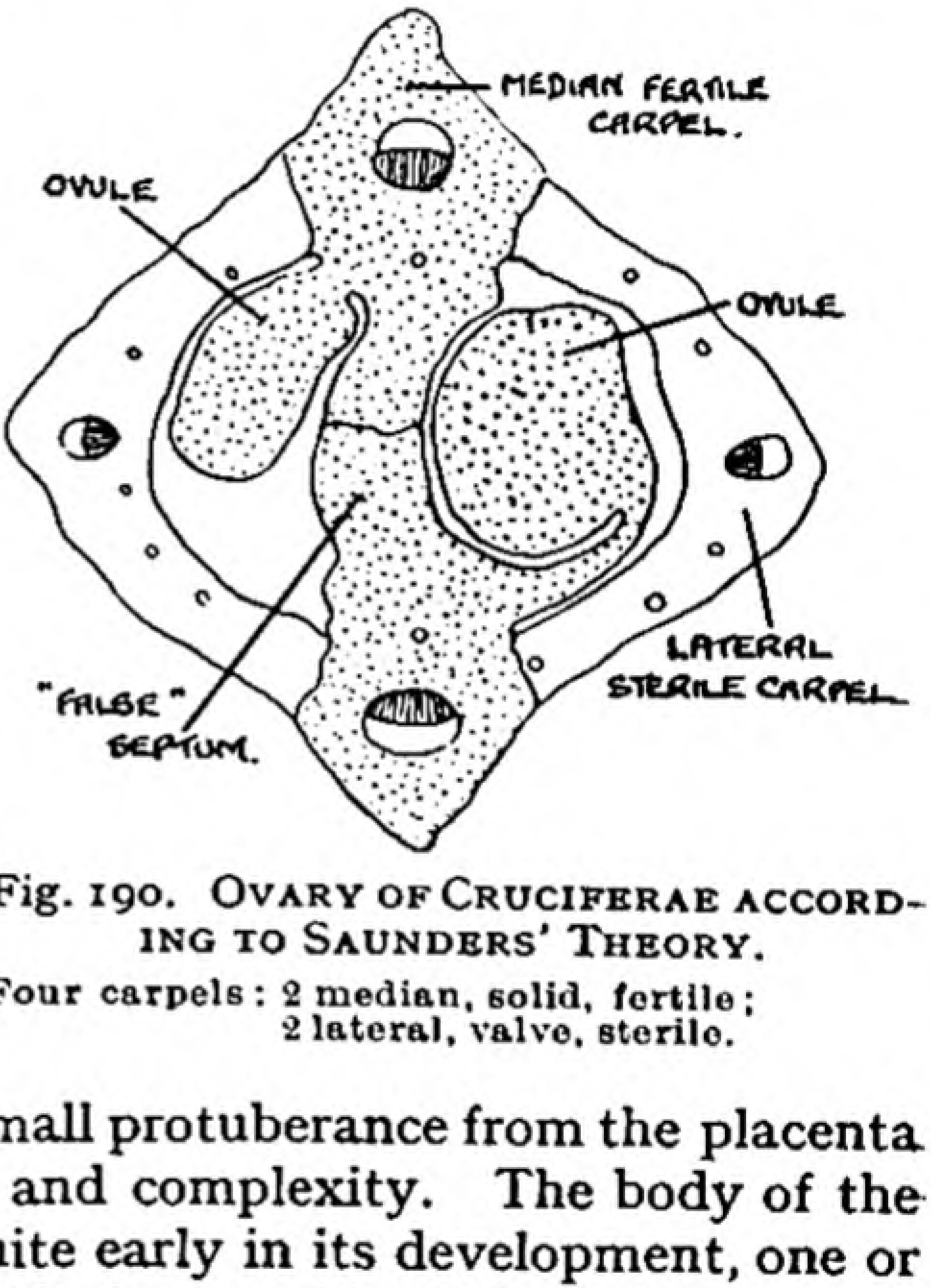


Fig. 190. OVARY OF CRUCIFERAE ACCORDING TO SAUNDERS' THEORY.
Four carpels : 2 median, solid, fertile ; 2 lateral, valve, sterile.

The young ovule arises as a small protuberance from the placenta and gradually increases in size and complexity. The body of the ovule is called the **nucellus.** Quite early in its development, one or two ridges of cell tissue appear at its base and in their further growth encroach over the still growing nucellus so as ultimately to enclose it, except for a small pore left at the apex which persists as the **micropyle.** The one or two coverings thus formed are the **integuments.** Meanwhile, from the basal region of the ovule, or **chalaza,** below the integuments, an elongation forms the **funicle,** or "stalk" of the ovule (Fig. 189). This joins the chalaza at the hilum.

At an early stage in the development of the nucellus a hypodermal cell at the apex enlarges (Fig. 191, A). It usually divides into two, an upper (outer) tapetal cell, and a lower (inner) spore-mother cell (Fig. 191, B). The nucleus of the latter divides twice, the division being meiotic, and cell-walls are formed. Of the four haploid cells thus resulting, only one is a functional megaspore.

The remaining three show no further development. Exceptionally, as in *Casuarina*, all four are functional.

The functional megaspore enlarges as the ovule grows, and comes to occupy the greater part of the nucellus (Fig. 192). Meanwhile, its nucleus divides into two daughter nuclei, one of which migrates to the micropylar, the other to the chalazal end of the megaspore. In these positions each nucleus divides further, giving rise to four nuclei at each pole. Three of the nuclei at the micropylar pole become surrounded by cytoplasm and form the two **synergidae** and the **oosphere** or **egg-cell** (female gamete). Three of the nuclei at the chalazal pole become surrounded by cytoplasm and cell-walls, and form the **antipodal cells.** The remaining two polar nuclei, one at each pole, migrate towards the centre of the megaspore, where they fuse to form the **secondary nucleus** (Fig. 189), often referred to as the primary endosperm nucleus.

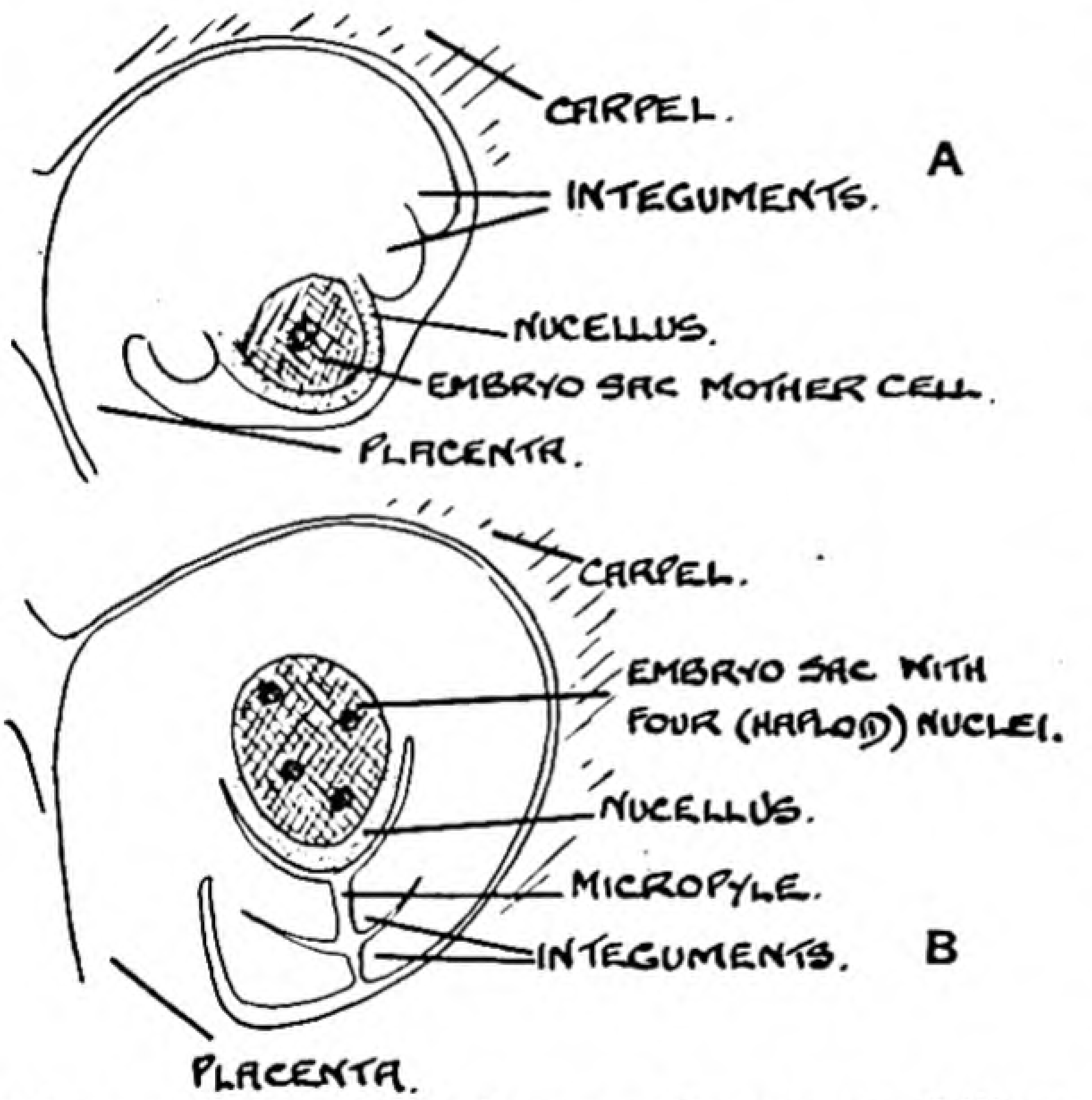


Fig. 191. DEVELOPMENT OF OVULE OF *Lilium*.
A, Hypodermal cell at apex of young nucellus;
B, Result of meiotic division giving 4 haploid nuclei.

Before cytological work revealed the true nature of the megaspore, it was known by the name **embryo-sac,** and it is still frequently referred to by this name.

28. Structure of the Mature Ovule

Fig. 192 illustrates the structure of the ovule of *Caltha* at the time when it is ready for fertilisation. The slender funicle attaches the ovule to the basal placenta of the ovary and carries a vascular bundle to the chalaza. The nucellus is invested by the two integuments, and the micropyle is seen as a narrow passage or pore at the apex. Almost filling the nucellus is the enlarged megaspore (or embryo-sac). Within the megaspore, at the micropyler end, are the three protoplasts of the egg-apparatus; one is the oosphere, the other two the synergidae. At the chalazal end are the three antipodal cells enclosed in cell-walls. In the centre of the megaspore is the secondary nucleus.

29. Forms of Ovule

There are several forms of ovule to be noticed. One is the **orthotropous** ovule (Fig. 189). Here the ovule is straight, not curved or bent appreciably. The chalaza and hilum lie close together, and the micropyle is at the extreme apex.

In the *inverted* or **anatropous** form (Fig. 192) the body of the ovule has bent over during development, and fused for some distance with the funicle. This fused portion of the funicle is called **the raphe**. In this form the micropyle and hilum lie close together, and the chalaza is towards the other end.

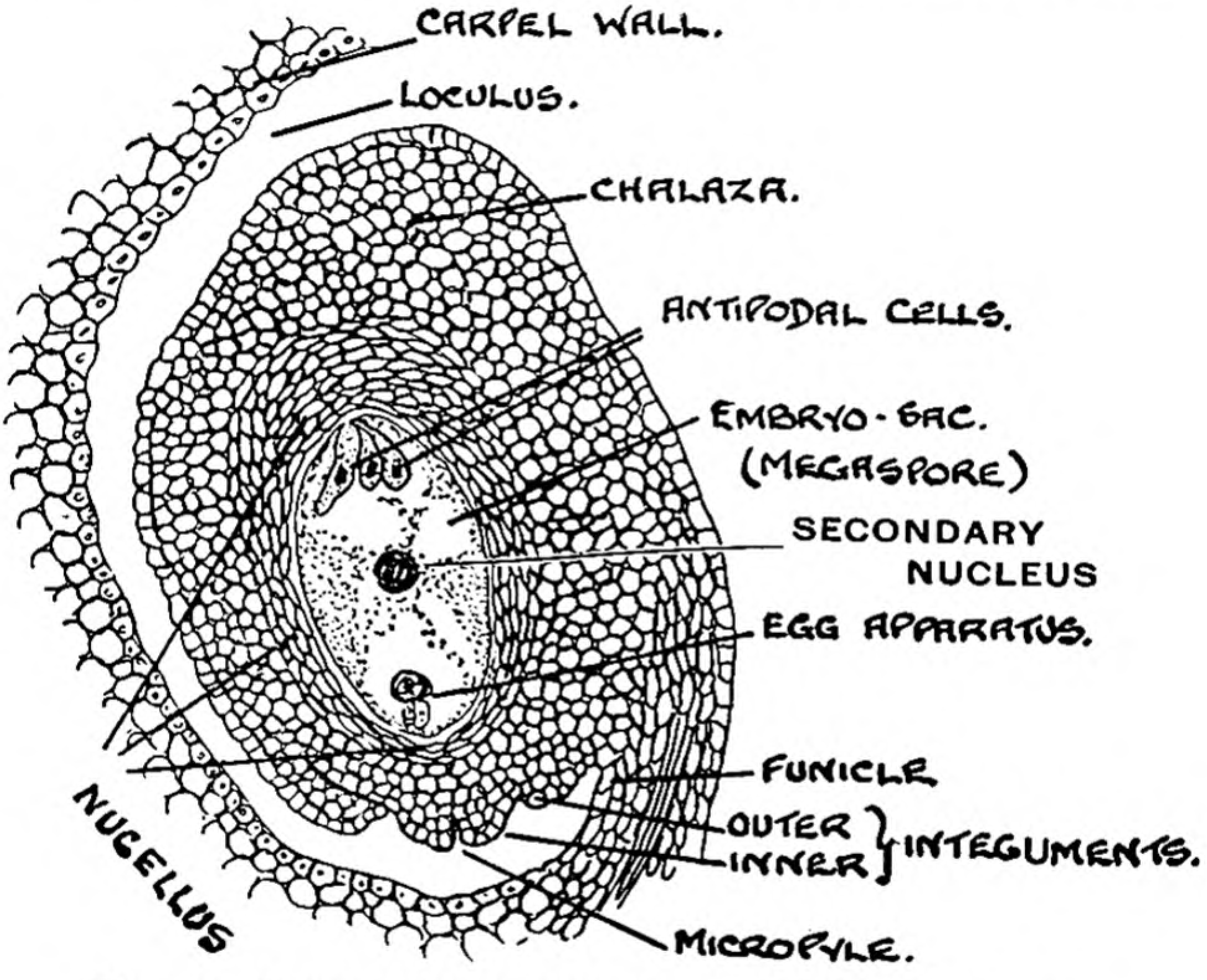

CARPEL WALL.
LOCULUS.
CHALAZA.
ANTIPODAL CELLS.
EMBRYO-SAC. (MEGASPORE)
SECONDARY NUCLEUS
EGG APPARATUS.
FUNICLE
OUTER
INNER
INTEGUMENTS.
MICROPYLE.
NUCELLUS

Fig. 192. Longitudinal Section, Anatropous Ovule of *Caltha*.

In the **curved** or **campylotropous** form (Fig. 193, A) the body is curved and bent round, so that the micropyle lies near the funicle; but there is no fusion with the funicle. Hilum, chalaza, and micropyle all lie close together. The **amphitropous** ovule is an intermediate form in which the body of the ovule is straight, but has been twisted round, so that its long axis is at right angles to the funicle (Fig. 193, B).

Of these forms the anatropous is most frequently met with. Examples of the campylotropous ovule are found in many Cruciferae and Papilionatae (pea, bean, etc.). The orthotropous ovule is less frequently found, e.g. *Polygonum* (Fig. 189). The Loganiaceae and some Cruciferae give examples of the amphitropous ovule.

30. Cohesion and Adhesion

The student must be clear as to the meaning of these terms. *Cohesion* is union between members of the same series of floral leaves. Thus gamosepalous, polysepalous, polyandrous, syngenesious, apocarpous, syncarpous are terms signifying cohesion or want of cohesion. *Adhesion* means union between members of different series, as when the stamens are epipetalous. We have already explained that cohesion or adhesion of parts in the flower is not due to the actual fusion of parts originally separate, but to common basal growth during development.

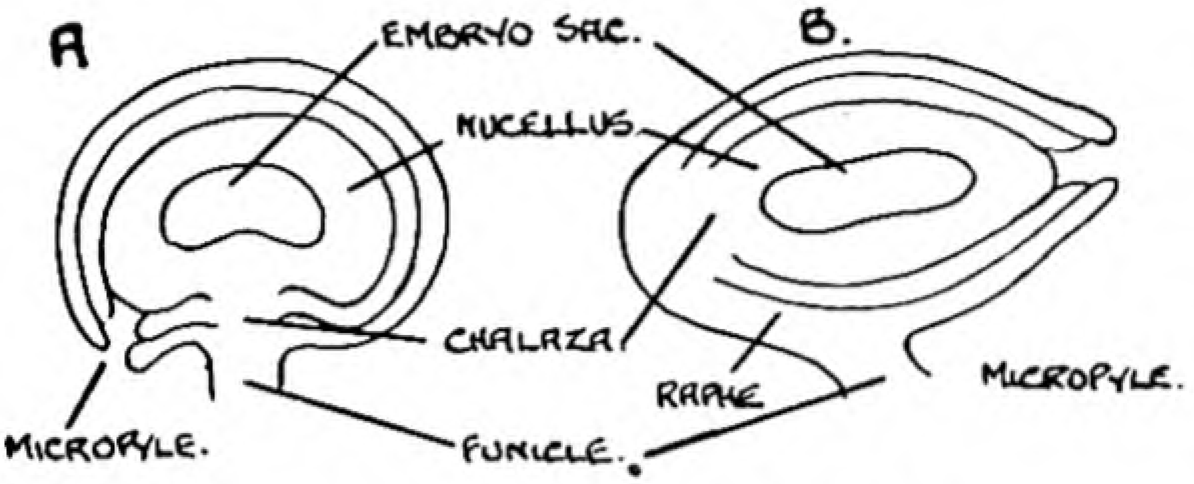


Fig. 193. Forms of Ovule.
A, Campylotropous ovule, e.g. Cruciferae; B, Amphitropous ovule, e.g. *Strychnos Nux-vomica*.

31. Vertical Sections and Floral Diagrams

The general structure and arrangement of parts in a flower may be shown in drawings of longitudinal or vertical sections [Figs. 174, 176 (half-flower), and 188 (half-flower)], in floral diagrams and floral formulae.

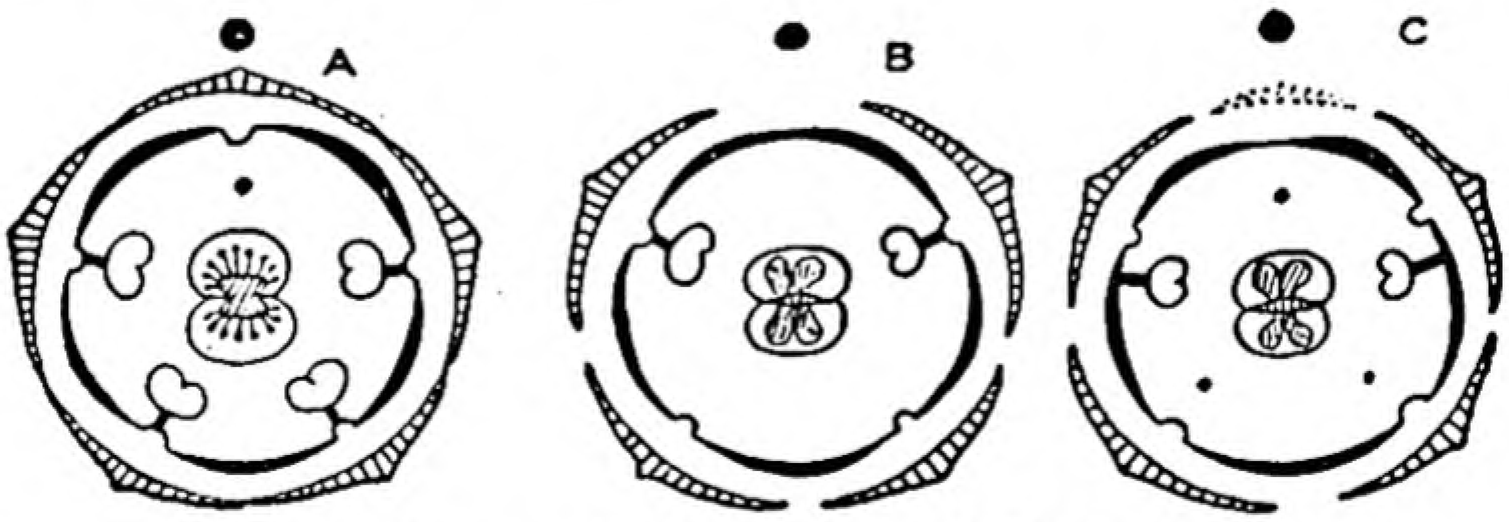


Fig. 194. Floral Diagrams of Scrophulariaceae.
A, *Digitalis*; B, Empirical diagram of *Veronica*; C, Theoretical diagram of *Veronica*.

The **floral diagram** may be described as a ground-plan of the flower showing the relation of the parts to each other and to the mother-axis. In making a floral diagram cohesion of parts may be indicated by connecting lines (Fig. 194, A), and this may also be done in the floral formula which should accompany the diagram. The aestivation may be indicated as in Fig. 195, A and B. An *empirical* diagram (Fig. 194, B) is one showing only the relative positions of the parts actually present. A *theoretical* one indicates, as well, by conventional means, the relative positions of parts which we assume were originally present, but are now lost (Fig. 194, C).

The **floral formula**, together with the diagram and longitudinal section, enables us to represent the essential *morphological* features of the flower without a word of description being necessary.

The symbols ⊕ and † respectively denote radially and bilaterally symmetrical (zygomorphic) flowers, the direction of the arrow indicating the plane of symmetry along which the flower can be divided into equal halves. The signs ♂, ♀, ☿ respectively denote staminate, carpellary, and hermaphrodite (" perfect ") flowers. The letters K, C, and P represent calyx, corolla, and perianth, A and G the androecium (stamens) and gynaeceum (pistil), and the figure following each letter gives the number of parts in each series. Cohesion is indicated by brackets enclosing the number of parts; a horizontal bracket ⌒ indicates adhesion between the parts of successive whorls; a horizontal line above the number after G means that the ovary is inferior, a line below, that it is superior; the symbol ∞ is used when there are numerous parts in any series.

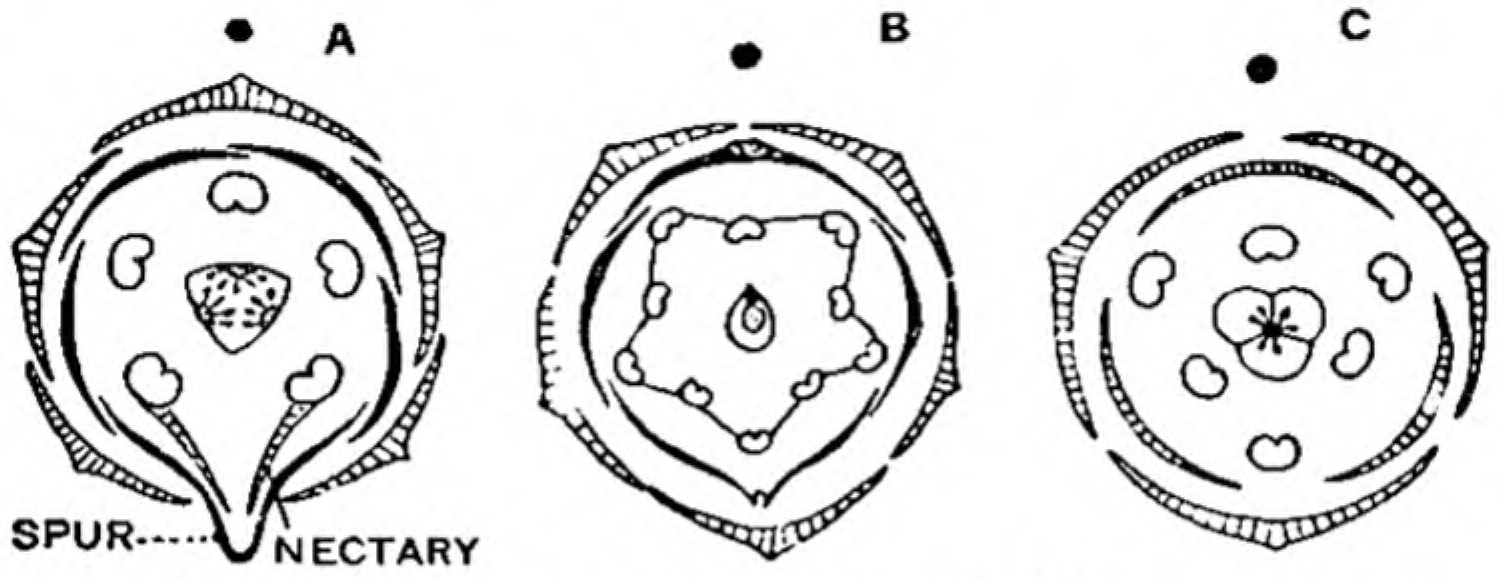


Fig. 195. FLORAL DIAGRAMS.

A, *Viola*; B, Papilionatae (monadelphous form); C, *Lilium*.

Thus the typical floral formula of Myrsinaceae

$$\text{☿}\ \oplus\ K(5)\ \overset{\frown}{C(5)\ A5}\ G(\underline{5})$$

reads—hermaphrodite, radially symmetrical flower, gamosepalous calyx of five sepals, gamopetalous corolla of five petals, androecium of five free epipetalous stamens, syncarpous pistil of five carpels with a superior ovary. The floral formulae of many common plants are given in Chap. XIII.

CHAPTER X

THE INFLORESCENCE

1. Introductory

The inflorescence is the part of a plant which is concerned with the production of flowers. It may or may not be distinct from the vegetative part. Thus, in some annual plants the entire branch-system of the shoot may be regarded as an inflorescence, whilst in biennials the second year's growth may be so regarded. Inflorescences are classified according to the type of branching into (*a*) indefinite or racemose and (*b*) definite or cymose. The leaves, whether ordinary vegetative leaves or modified ones which subtend the flowering branches are termed bracts. In racemose inflorescences the growing point of the primary axis does not terminate in a flower, but, throughout its growing period, it is continually developing the axis and new lateral members, *i.e.* it is a monopodium, whereas in cymose inflorescences (sympodia) the primary axis and the successive daughter axes terminate in flowers. It is, of course, possible for the primary axis to be monopodial, and the lateral branch-systems to be sympodial, thus forming a compound racemo-cymose inflorescence.

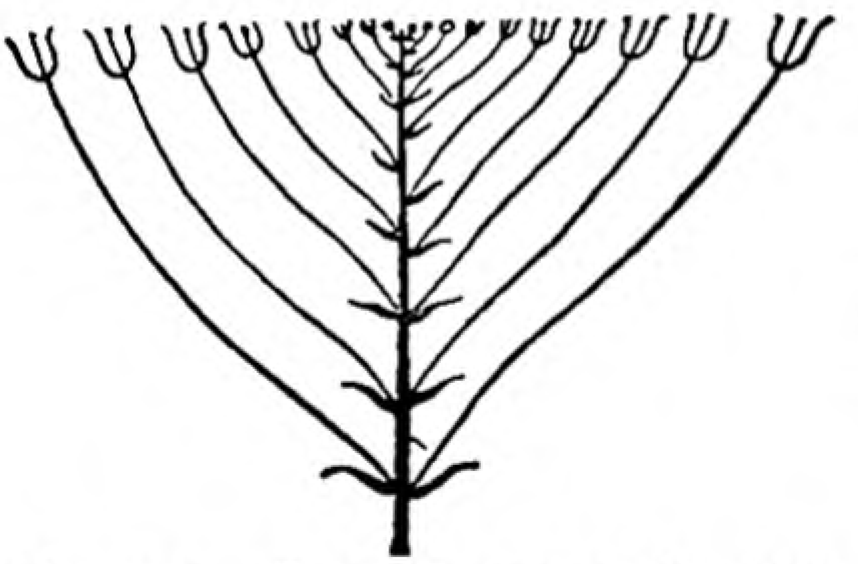


Fig. 196. Diagram of a Corymb.

2. Simple Racemose Inflorescences

Of these we recognise four chief types:—

(*a*) The **typical raceme** (Fig. 173), in which the mother-axis (peduncle) is elongated, and the flowers are stalked (pedicellate). Examples are found in *Crotalaria* and many orchids.

Similar to this in essential characters is the **corymb**, which may be regarded as a modification of the typical raceme. The mother-axis is relatively shorter, and, owing to the elongation of the lower pedicels, all the flowers come to one level (Fig. 196). This renders the whole inflorescence more conspicuous to insects, and the individual flowers tend to remain small. Good examples are found in many Cruciferae (e.g. candytuft).

Inflorescences intermediate in character between the corymb and typical raceme are described as corymbose racemes, e.g. the wallflower, in which the inflorescence is corymbose when young, but lengthens out when fruiting.

(*b*) The **spike** is a racemose inflorescence in which the mother-axis is elongated, and the flowers are *sessile* (Fig. 197), e.g. spotted orchid and *Plantago*. By this arrangement small flowers may be aggregated in a cylindrical mass.

There are one or two special forms of the spike. The **spadix** is a massive fleshy spike, bearing small, usually unisexual flowers occurring especially in the Araceae. It is protected by a large enveloping bract, sometimes green, more usually petaloid, known as a *spathe*. The spathe and upper part of the spadix serve to attract insects, and sometimes, as in *Arum maculatum* (Fig. 198), there is a fly-trap mechanism in connexion with the pollination of the flowers. The **catkin** (Fig. 199) is generally a long, more or less pendulous, deciduous compound spike, bearing unisexual flowers. It is found in many nut-bearing and other trees, e.g. birch, hazel, poplar. The male catkin as a rule hangs loosely in the air so that the microspores (pollen), protected from rain by the catkin scales, are readily blown out by the wind when dry.

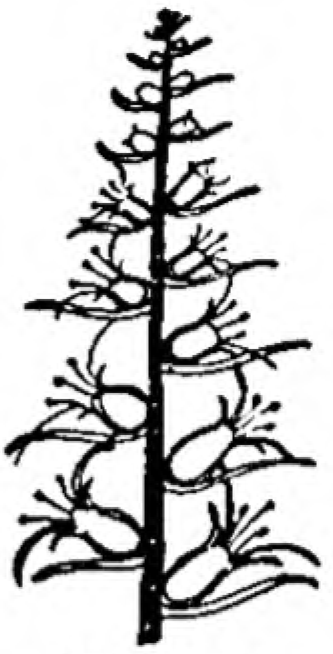


Fig. 197. DIAGRAM OF A SPIKE.

(*c*) The **umbel** (Fig. 200) is a racemose inflorescence in which the flowers are stalked, but, owing to the abbreviation of the mother-axis, are given off at one level. The indefinite growing point develops a large number of lateral flowers, but does not give rise to an elongated mother-axis. Each flower of the umbel may be subtended by a bract, the collection of bracts forming the **involucre** of the umbel.

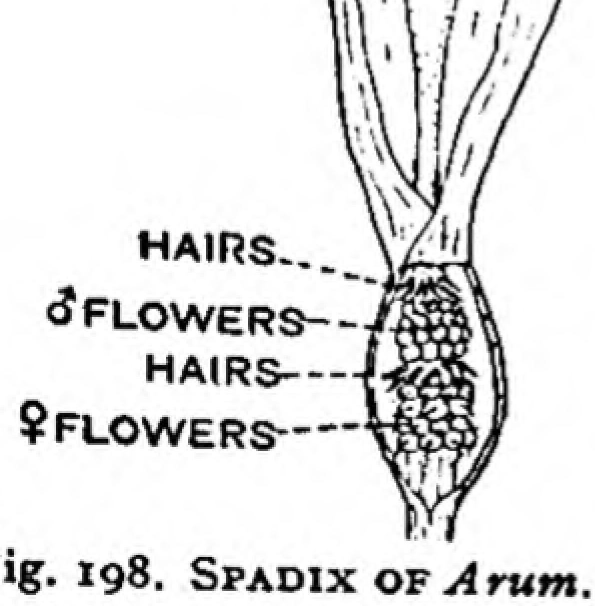


Fig. 198. SPADIX OF *Arum*. Part of lower end of spathe removed to expose the flowers.

(*d*) The **capitulum** (Fig. 201) is a racemose inflorescence in which the flowers are sessile, and crowded together on a reduced or abbreviated mother-axis which is called the *disc*. It is sometimes flat, more frequently dilated and convex or conical. Examples are found chiefly in the Compositae (Fig. 201). The student must clearly recognise that the heads of the daisy, dandelion, etc., are not single flowers, but inflorescences bearing a large number of sessile flowers or florets. The capitulum is invested by a number of small scaly, overlapping, barren bracts, together forming the **involucre**. Bracts (or paleae) may also subtend the individual florets as in *Anthemis nobilis* (chamomile).

The massing together of small flowers in the umbel and capitulum has the same biological significance as in the corymb.

3. Cymose Inflorescences

These are usually either *uniparous* or *biparous* (see p. 73). In uniparous (or monochasial) forms each successive axis ends in a flower after producing one daughter-axis. Four different types are recognised: the bostryx, drepanium, cincinnus and rhipidium (Fig. 49). They are *sympodial*, and sometimes resemble typical racemes (see Fig. 49, B, D). Uniparous cymes resembling racemes can be distinguished by the fact that the bracts, if they are present, are on the opposite side of the sympodial axis from the leaves. If bracts are not developed they are not easily distinguished.

In *biparous* cymes each axis ends in a flower after producing two daughter-axes. It is also called a **dichasium** (Fig. 202). Typical examples are found in many Caryophyllaceae. Sometimes the daughter-axes are not given off at the same level, e.g. some *Ranunculus*, *Helleborus*, etc.

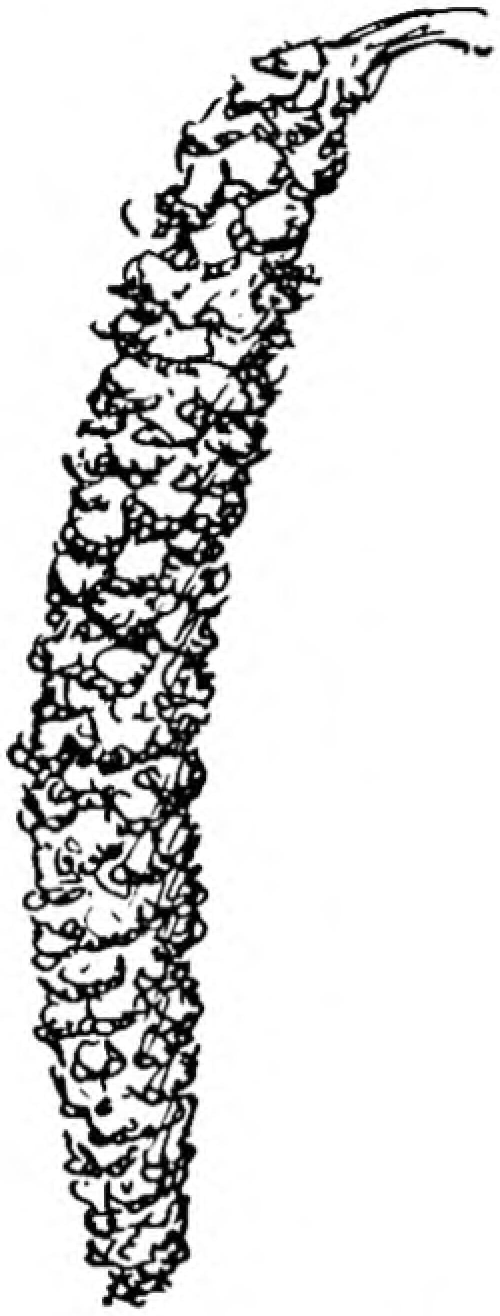


Fig. 199. MALE CATKIN OF HAZEL.

4. Compound and Mixed Inflorescences

Many inflorescences are **compound,** e.g. a raceme of racemes, (e.g. *Delphinium*), or spikelets (e.g. *Triticum*), or an umbel of umbels (e.g. most Umbelliferae). The *compound umbel* (Fig. 203), in addition to the bracts at the base of the chief branches constituting the *involucre*, may have smaller bracts at the base of each secondary umbel, the *involucel.*

Many inflorescences are **mixed.** We may, for example, have a raceme of spikes, a raceme of capitula, a spike of capitula, a raceme of cymes. etc. The raceme of *spikelets, i.e.* the *panicle,* is a common form in many grasses (e.g. oat); in *Aesculus* there is a raceme of short cymes (cincinni). In *Syringa* the inflorescence is of the same nature, but the branching is much more copious.

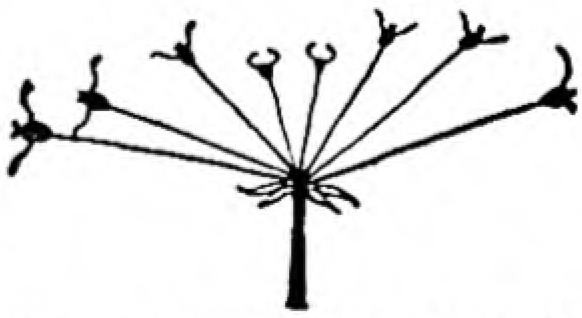


Fig. 200. DIAGRAM OF A SIMPLE UMBEL.

5. Special Forms

There are many inflorescences which, owing to abbreviation of axes or special crowding of the flowers, do not so readily yield to careful analysis. In *Crataegus*, for example, the inflorescence might be mistaken for a typical corymb. Examination will show, however, that the lateral axes borne on the main axis are really cymes. It is a *corymbose cyme*.

Similarly the globular inflorescences of *Hydrangea* and of the snow-ball tree (*Viburnum opulus*) are corymbose cymes, rendered conspicuous by the petaloid calyces and enlarged corollas of flowers specialised for this purpose. In horticultural varieties all the flowers are sterile.

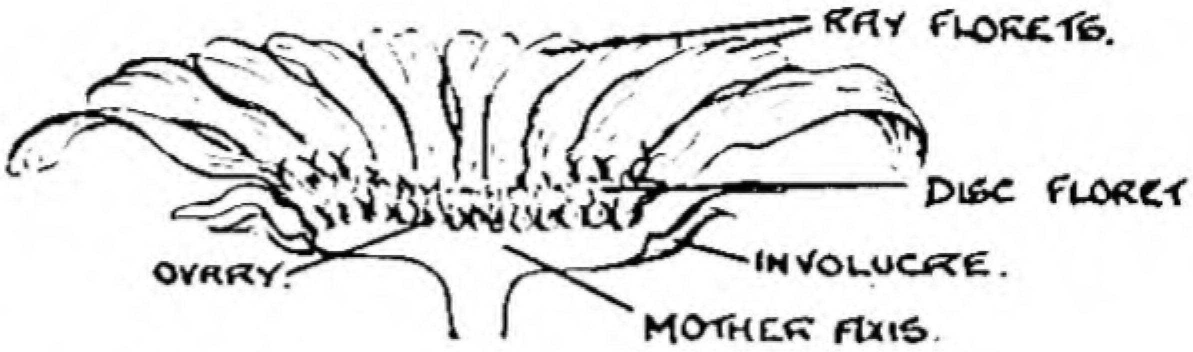


Fig. 201. CAPITULUM OF *Aster* CUT LONGITUDINALLY.

In the cultivated geranium (*Pelargonium*) and many species of *Narcissus* the inflorescence, at first sight, appears to be an umbel. But it will be found that the young flowers are not by any means aggregated towards the centre, and that the flowers are arranged in a number of groups. These are really cymose clusters. We may speak of the whole inflorescence as an *umbellate cymose head*. These are found in many plants. In *Narcissus* the inflorescence is protected by a membranous *spathe*.

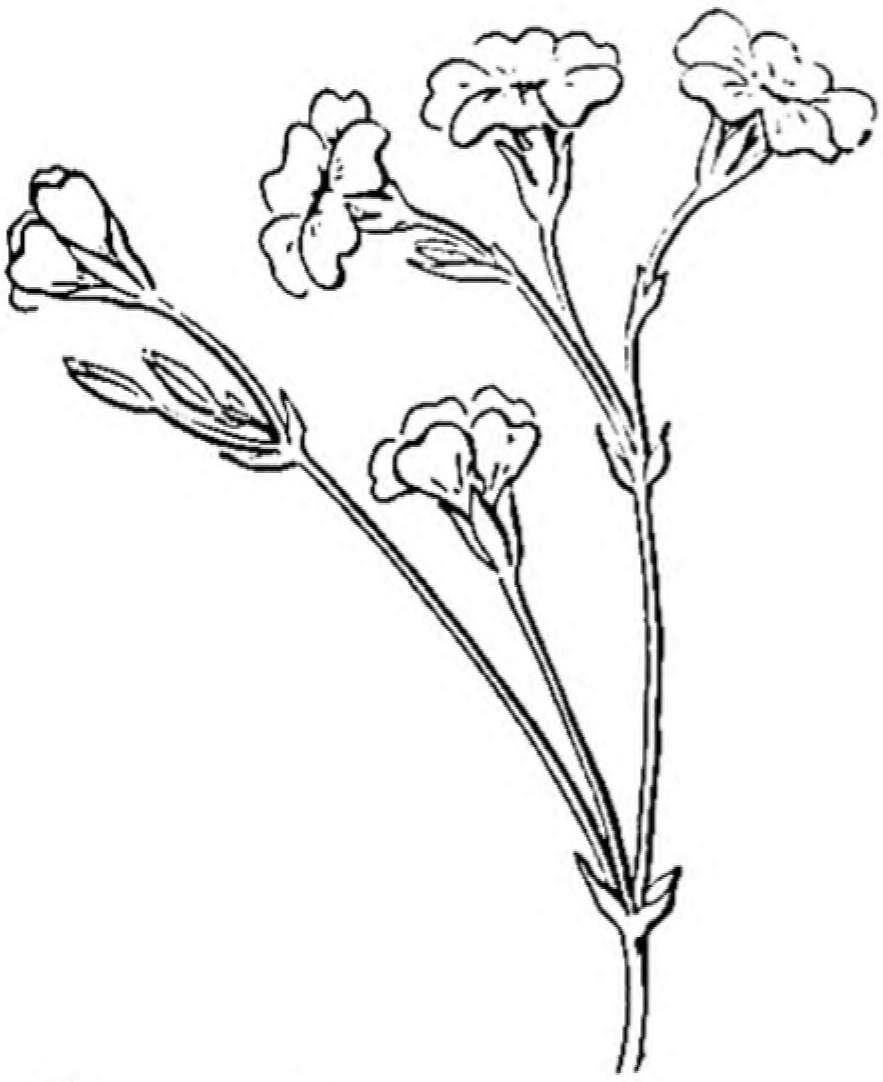


Fig. 202. DICHASIUM OF *Cerastium*.

In deadnettle (*Lamium*) and many other members of the Labiatae, the leaves are opposite and decussate, and at each node there seems to be a whorl of flowers. These *apparent* whorls are called **verticillasters** (Fig. 204). Careful analysis shows that there is in the axil of each leaf an inflorescence which is a dichasium of cincinni, *i.e.* a biparous cyme which passes on either side into a uniparous form by suppression of one of the branches at each branching. It is difficult to recognise this because the axes have been reduced and the flowers are sessile. It is easily recognised in many Labiatae where the flowers have short stalks. In Fig. 205 the axis which ends in flower 1 gives rise to two daughter-axes, 2, ending in flowers. Each of these gives rise to an axis, 3, and so on.

In *Dianthus barbatus* (Caryophyllaceae) and some other plants there is a copiously branched biparous cyme, in which the axes are short and all the flowers crowded together.

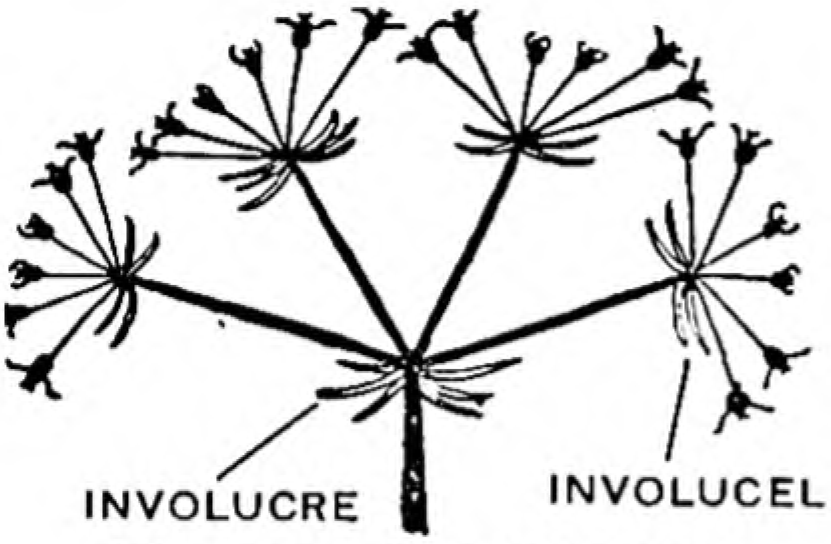


Fig. 203. Diagram of a Compound Umbel.

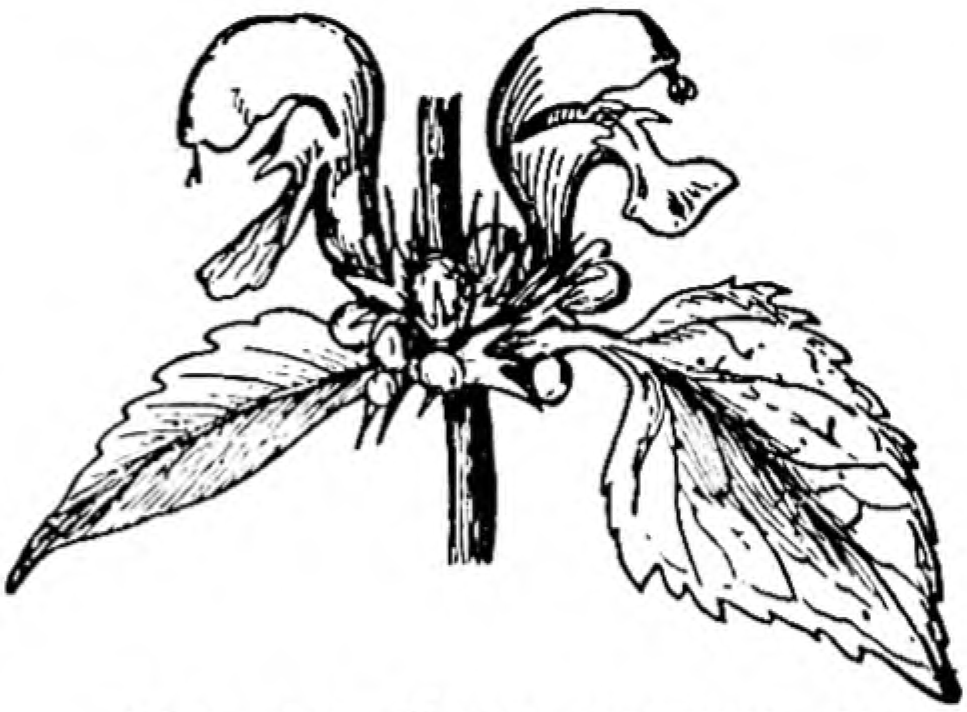


Fig. 204. Verticillaster of Deadnettle.

The **cyathium** (Fig. 206) is a peculiar inflorescence found in *Euphorbia* (spurge). There is a cup-shaped involucre, the margin of which bears a number of crescent-shaped glandular scales. Inside the cup there are several stamens; also a gynaeceum borne on a stalk. Careful examination shows that each stamen is really a male or staminate flower. This is borne out by the fact that each stamen is articulated to a stalk and has a scaly bract at its base. The gynaeceum with its stalk is a female flower. The stamens are arranged in five groups, which are reduced cincinni, around the female flower. Thus an inflorescence looks like a single flower.

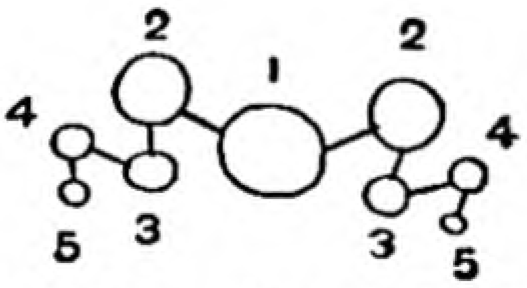


Fig. 205. Diagram indicating the relation of Flowers in half of a Verticillaster.

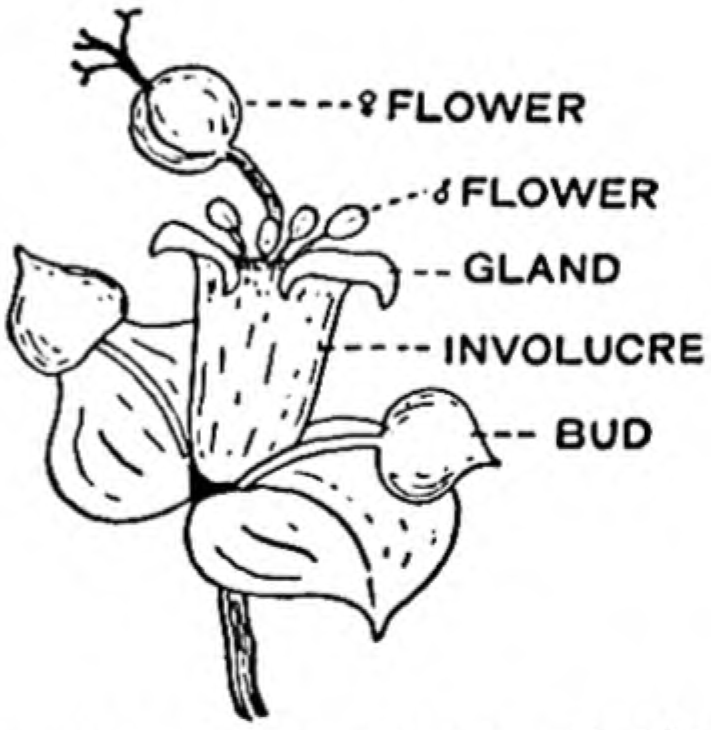


Fig. 206. Cyathium of *Euphorbia*.

CHAPTER XI

REPRODUCTION AND LIFE HISTORY OF THE ANGIOSPERM

1. Introduction

In the preceding chapters we have considered the great variety of form and structure met with in the organs of angiospermous plants. Such plants develop either from specialised parts of the vegetative shoot which directly develop into new plants resembling the parent, *i.e.* by **vegetative reproduction** or **propagation**; or form seed involving a **sexual** process. We have already referred to and described various methods of vegetative reproduction in the sections dealing with modifications of stems and roots. We have also noticed the structure and germination of various seeds. We must now consider in more detail the processes which lead to the formation of seed and fruit.

2. Pollination

In order that seed may be produced, the microspores (or pollen-grains) must be transferred from anthers to stigma. This transference is called **pollination.** It is convenient to retain this term on account of long usage, and to refer to the microspores in the collective sense as pollen. There may be (*a*) **self-pollination**; or (*b*) **cross-pollination.** In the former, the microspores either fall, or are transferred in some way, from the anthers to the stigma or stigmas *of the same flower*. In the latter, they are carried in various ways to the stigma or stigmas *of other flowers*, either on the same plant, or on different plants of the same species. As pollination is followed, later, by the process of fertilisation, the terms *self-fertilisation* (**autogamy**) and *cross-fertilisation* (**allogamy**) are often used. Pollination and fertilisation are, however, two distinct processes, and should be carefully distinguished.

The great majority of Angiosperms have hermaphrodite flowers, yet cross-pollination is common in hermaphrodite flowers, because most of them are so constructed as to secure it.

Self-pollination is also of frequent occurrence in hermaphrodite flowers, even in many which appear to be constructed for cross-pollination; and cases are not uncommon where special arrangements are made for self-pollination.

Cross-pollination may be effected by various agencies. Thus, the microspores may be transferred by means of the wind, water, or animals, and the flowers are said to be **anemophilous, hydrophilous,** or **zoophilous** respectively. Grasses, members of the Betulaceae, Fagaceae and Urticaceae, are examples of anemophilous flowers. Hydrophilous flowers are found in a few water-plants; but most aquatic plants raise their flowers well out of the water and are pollinated by wind or by insects. While we have examples of flowers being pollinated by means of such animals as slugs, snails, humming-birds, etc., the animals thus employed are, in nearly all cases, insects (flies, moths, bees, etc.). Such flowers are said to be **entomophilous.** The great majority of angiospermous flowers are such. Here we recognise an intimate interrelation existing between the plant and animal kingdoms.

3. Contrivances and Conditions favouring Cross-pollination

There are in flowers many arrangements and mechanisms which ensure cross-pollination. Usually such arrangements and mechanisms merely give chances in favour of cross-pollination without precluding the possibility of self-pollination. Sometimes, however, they make self-pollination difficult, or altogether impossible.

In plants with unisexual flowers, of course, cross-pollination is absolutely necessary if seed is to be produced. We have this condition in its extreme form in dioecious plants, e.g. *Salix* (willow). There are a few plants, also, in which cross-pollination must take place if seed is to be produced, because the plants are *self-sterile, i.e.* the flower cannot be fertilised by its own microspores; this occurs in some specimens of *Passiflora* (passion-flower), of *Lobelia,* and of *Abutilon.* In some flowers, again, self-pollination may be rendered unlikely or difficult owing to the relative position of anthers and stigma.

A condition of much more general occurrence is that known as **Dichogamy.** This is a condition in which the anthers and stigma in hermaphrodite flowers come to maturity at different times, and which, when completely developed, entirely prevents self-pollination.

There are two forms of dichogamy: (*a*) **protandry,** in which the anthers ripen first, so that when the microspores are shed the stigma of the same flower is not ready to receive them; in this case, if the microspores are not to be wasted, they must be transferred to an older flower; (*b*) **protogyny,** in which the stigma ripens first; here the microspores must be transferred to a younger flower. Protandrous flowers are much more common than protogynous. Examples of the former are found in Compositae, Labiatae, Umbelliferae, Solanaceae, etc.; of the latter in *Plantago, Luzula,* some Scrophulariaceae, Ranunculaceae, etc. Wind-pollinated flowers are more often protogynous than protandrous, but many are unisexual.

Anemophilous and entomophilous flowers have each special characters of their own, so that as a rule we can distinguish them at a glance. In *anemophilous flowers*, the microspores are usually dry and smooth, and produced in great abundance, as much must be wasted; the flowers are small and inconspicuous; there is no nectar or perfume; and frequently the stigmas are branched and feathery, to catch the microspores. In many trees which are wind-pollinated the flowers appear in spring before the leaves, so that the microspores have free access to the flowers. In most herbaceous plants with wind-pollinated flowers, the latter are carried up on a long stem, well above the leaves, so as to expose them as freely as possible to the wind (e.g. *Plantago*, Chenopodiaceae, grasses, etc.).

Much greater variety of adaptation is shown by *entomophilous flowers*. As a rule they have large, conspicuous, or highly-coloured corollas, or are arranged in conspicuous inflorescences; they usually secrete nectar and give out perfume. The microspores are usually rough and sticky, and often not produced in any great abundance, as they are more sure of transference. The bright corollas, the perfume and nectar serve to attract insects which visit the flower in search of food.

A nectarless but otherwise insect-attracting flower is sometimes called a "pollen-flower." Examples are found in *Papaver*, *Rosa*, *Helianthemum*, *Anemone*, *Clematis*, *Hypericum*, *Ulex*, *Cytisus*, *Ulmaria*. These flowers are visited by pollen-feeding insects.

Many entomophilous flowers are further characterised by the presence of ingenious mechanical devices, which guide and control the movements of the insect and turn them to the best account. Thus, in many cases, the corolla is so constructed that the insect must alight on the flower or enter it in a special way (e.g. Labiatae, Papilionatae); the same result may be attained by the secretion of nectar into special receptacles or spurs (e.g. in *Viola*, Fig. 209). Often the insect, on entering a flower, pushes against special processes or outgrowths which move the stamens and bring the anthers in contact with its body (e.g. *Salvia*, sage, Fig. 210); or the stamens may be jerked, and the microspores scattered over the insect's body. In some flowers the stamens move in response to touch by a visiting insect. This is seen in *Centaurea jacea* where the filaments contract and pull the tube formed by the syngenesious anthers backwards over the style, and the microspores are thus swept out and exposed. Curvature movements of stamens in response to a shock stimulus are seen in a number of Families such as Berberidaceae, Tiliaceae, Cactaceae and Cistaceae. Also sensitive stigmas may close over the deposited microspores as in Scrophulariaceae.

Frequently spots or lines of a conspicuous colour are developed on the corolla; these have been called "honey-guides," as they are believed to afford insects guidance in seeking out the nectar.

The general result of all these devices is that the insect receives pollen on a special part of its body, and when it enters another flower the pollen is deposited on the stigma. In many protandrous flowers this is secured by the style bending over so that the stigma is in the position formerly occupied by the stamens.

A special, but at the same time simple, arrangement for ensuring cross-pollination by insects is known as **heterostyly.** It is seen in primrose (Fig. 207). Here there are two types of flower, borne on different plants. One kind (thrum-eyed) has long stamens (with anthers in the throat of the corolla tube) and a short style; the other (pin-eyed) has a long style and short stamens; thus in the two types the positions of anthers and stigma are reversed. Pollination is effected by transference between these two forms and not between two flowers of the same form. This is the dimorphic form of heterostyly. In purple loosestrife (*Lythrum*) there are three types of flower combining two positions for the stamens and one for the stigma (Fig. 208). Such flowers are said to be trimorphic.

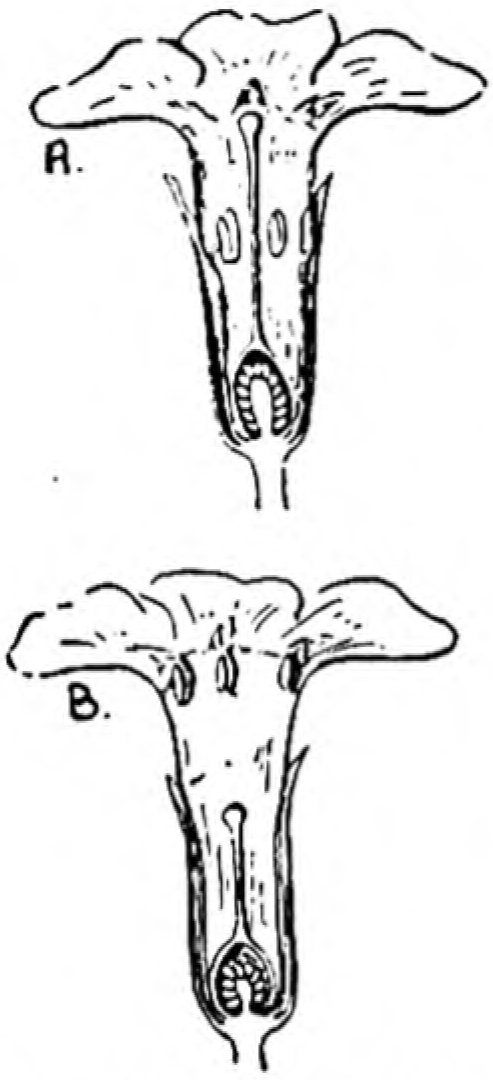


Fig. 207. DIMORPHISM IN *Primula*.

A, Pin-eyed; B, Thrum-eyed form in longitudinal section (half-flowers).

Trimorphism is also seen in species of *Oxalis* and dimorphism in *Turnera* and species of *Jasminum*.

4. Insects that Visit Flowers

The chief flower-visiting insects are beetles (Coleoptera), flies (Diptera), bees and wasps (Hymenoptera), butterflies and moths (Lepidoptera). In connexion with the pollination of flowers, the important differences to be noticed between these insects are the size of the body, the length of the tongue (proboscis), the time of year at which each kind is most plentiful, and their habits—e.g. whether they collect pollen or nectar or both, whether they fly by day or in the evening. By carefully studying the structure of a flower, and noting such points as the time of flowering, the order in which the anthers and stigmas mature, the relative positions of anthers and stigmas in the open flower and any changes in position that may occur, we can often tell what kind of insect is capable of effecting cross-pollination, and whether or not self-pollination is possible.

Most flies and beetles have very short tongues, usually less than 3 mm. long. Most of the larger and longer-tongued flies, e.g. gadflies, "cleggs," and horseflies do not visit flowers; but there are some, chiefly hover-flies and bee-flies, with tongues sometimes as long as 12 mm., which are regular flower-visitors.

Flowers may be arranged in various biological groups or classes according to their adaptations for insect-visitation:—

(1) **Flowers adapted for Short-tongued Insects.**—These may be (*a*) flowers in which the nectar is freely exposed on the surface, e.g. Umbelliferae, Rutaceae, etc.; (*b*) flowers with a very short tube, e.g. moschatel, bed-straw, enchanter's nightshade; (*c*) shallow open flowers such as stonecrop and saxifrages. Such flowers are visited by the shorter-tongued beetles and flies.

(2) **Flowers with Partially-concealed Nectar.**—This group includes flowers in which the nectar can be reached only by insects with tongues at least 3 mm. in length, and which are therefore visited by the longer-tongued beetles and flies, as well as by insects of higher type. The nectar may be slightly concealed by the stamens, e.g. *Ranunculus* and Myrtaceae; by the erect stiff sepals, as in the smaller Cruciferae; by the formation of a shallow calyx-tube, as in many Rosaceae; by a short corolla tube, e.g. the shorter-tubed Compositae, etc.

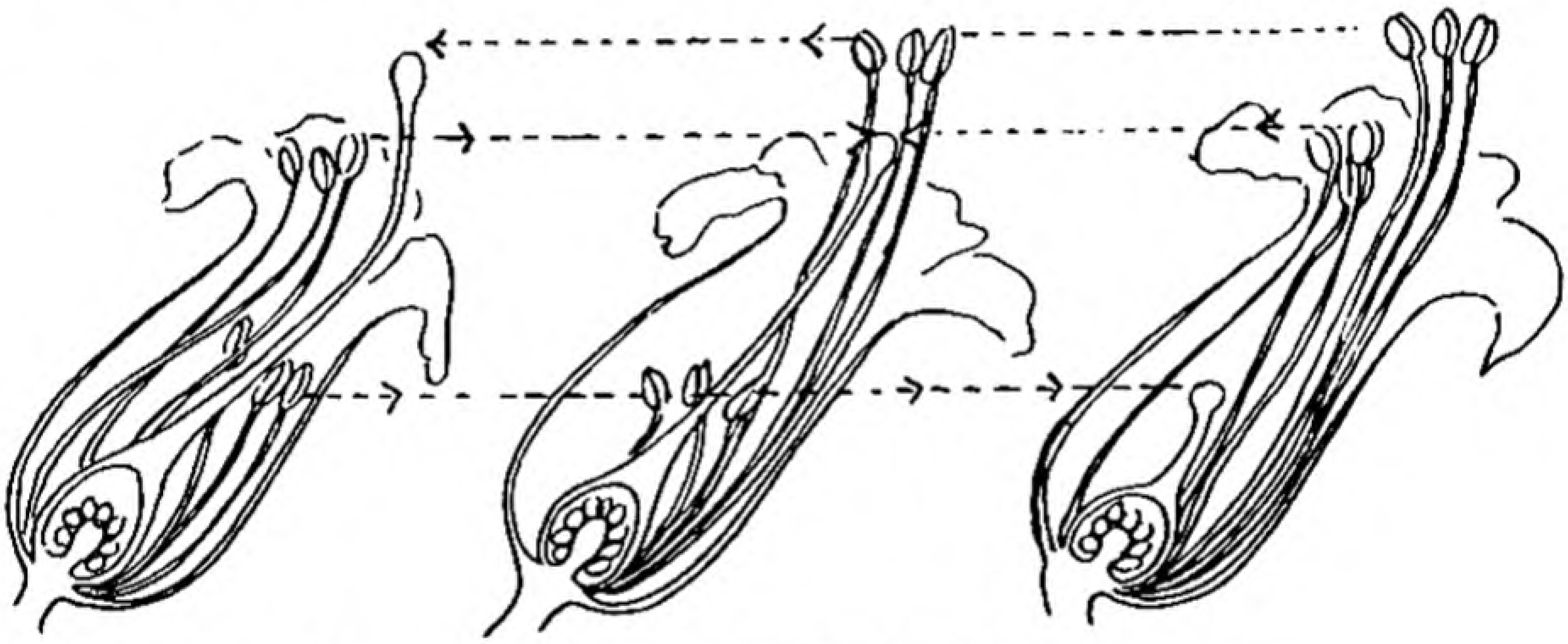


Fig. 208. *Lythrum Salicaria*, TRIMORPHISM.
Three types of flower.

(3) **Flowers with Fully-concealed Nectar.**—This type of flower differs only in degree from the last. Here the nectar can only be reached by insects having tongues about 6 mm. long, including the longest-tongued flies (chiefly hover-flies), the shorter-tongued bees, and wasps. The concealment of the nectar is effected by a further deepening of the flower, owing to the formation of a calyx-tube, to the calyx being gamosepalous or the corolla gamopetalous, or to other causes. Examples of these medium-tubed flowers are seen in some Rosaceae, Solanaceae, Scrophulariaceae, etc.

(4) **Long-tubed Flowers.**—When the flower-tube becomes longer, all the shorter-tongued insects are more or less completely excluded, and the flower is adapted for, and chiefly visited by, the larger bees, butterflies, and moths.

Many flowers belonging to the Amaryllidaceae, Iridaceae, Orchidaceae and Scitamineae, in which the perianth nearly always forms a long tube, come under this type. Flowers like those of Papilionateae, *Antirrhinum*, and *Calceolaria*, can only be opened by large bees, and only the longest-tongued bees can reach the nectar in such flowers as *Aconitum* and *Delphinium*.

Humble- and hive-bees have the most perfect mechanism (the " pollen-baskets " on the hind-legs) for collecting pollen to mix with nectar and feed their broods. Humble-bees have longer tongues than hive-bees, and are particularly skilful in finding the way to well-concealed honey.

Blue, purple, and red colours are often associated with flowers visited by bees (especially blue and purple) and butterflies (especially red), while flowers visited by other insects are usually white, yellow, or variegated; but there are far too many exceptions to allow of a general rule.

Birds, especially small honeysuckers and humming birds, may be active as pollinators. Flowers may be visited by both insects and birds, but bird-pollinated flowers generally show brilliant colour contrasts. Examples are afforded by *Strelitzia regina*, many species of *Protea*, *Salvia* species, *Loranthus aphyllus*, and some *Acacia* species.

(5) **Butterfly- and Moth-flowers.**—When the flower-tube (or at any rate the level of the nectar) is more than about 12 mm. (about half an inch) deep, the nectar is beyond the reach of bees, though they may visit the flower for pollen, or the humble-bee may bite through the tube (calyx or corolla) and thus rob the flower of its nectar. Butterflies may visit many flowers which are adapted for bees, *most* butterflies and moths having tongues of about the same length as, or a little longer than, those of bees.

Some moths, however, have far longer tongues (30 mm. or more in British species), which are (as in butterflies) carried coiled up in a spiral under the head when flying. These moths can reach nectar when it is at the bottom of a very long tube, as in *Lonicera*, which is visited chiefly by the night-flying privet hawk-moth, and the white convolvulus, which is pollinated by another species of hawk-moth (*Sphinx convolvuli*, tongue 80 mm. long). Other flowers pollinated by night-flying moths are *Oenothera*, *Nicotiana*, *Ligustrum*, and *Cereus*. Moth-pollinated flowers are generally white or pale-coloured, sweetly scented, and open in the evening, usually remaining closed and almost scentless during the day.

5. Examples of Floral Mechanism

(*a*) In the garden pansy (*Viola altaica*, Fig. 209) the anthers of the five stamens are firmly joined by hairs on their edges, and the two anterior stamens bear processes, functioning as nectar-glands, which pass down into the spur of the anterior petal. A space or chamber (" pollen-box ") is enclosed above the ovary, at the base of the style, by the five membranous scales borne on top of the anthers. The stigma, which projects beyond the anther-scales, is dilated and hollow. It has a tuft of hairs on each side, and below there is an opening into it, the lower edge of which is protected by a lip or flap (the " scraper ").

The flowers are pendulous, and hence the pollen, which is shed on the inner faces of the anthers, and is dry and loose, not sticky as in most entomophilous flowers, falls into the "pollen-box," from which it can escape only through the opening between the scales of the two anterior anthers.

The flowers are pollinated by long-tongued bees (and butterflies). When the insect enters the flower, pollen obtained from another flower may be deposited on the stigma, and cross-pollination thus effected. Pushing down into the spur of the anterior petal to reach the nectar, the insect receives a supply of pollen which has escaped from the "pollen-box." The "scraper" prevents this pollen being deposited on the stigma as the insect retires.

The conspicuously coloured centre of the flower, and the honey-guides on the lateral and spur petals serve to attract desirable insects. The entrance of small undesirable visitors is hindered by the hairs on the lateral petals and on the sides of the stigma, by the hairs lining the entrance and cavity of the spur, and by the length of the spur itself.

In *Salvia* (sage), one of the Labiatae, an interesting mechanism is found (Fig. 210). The corolla is bilabiate. The conspicuous lower lip attracts insects, and acts as a landing-place. The arched upper lip protects the stamens and style. There are only two stamens, the other two, characteristic of the Labiatae, being represented in the sage by staminodes.

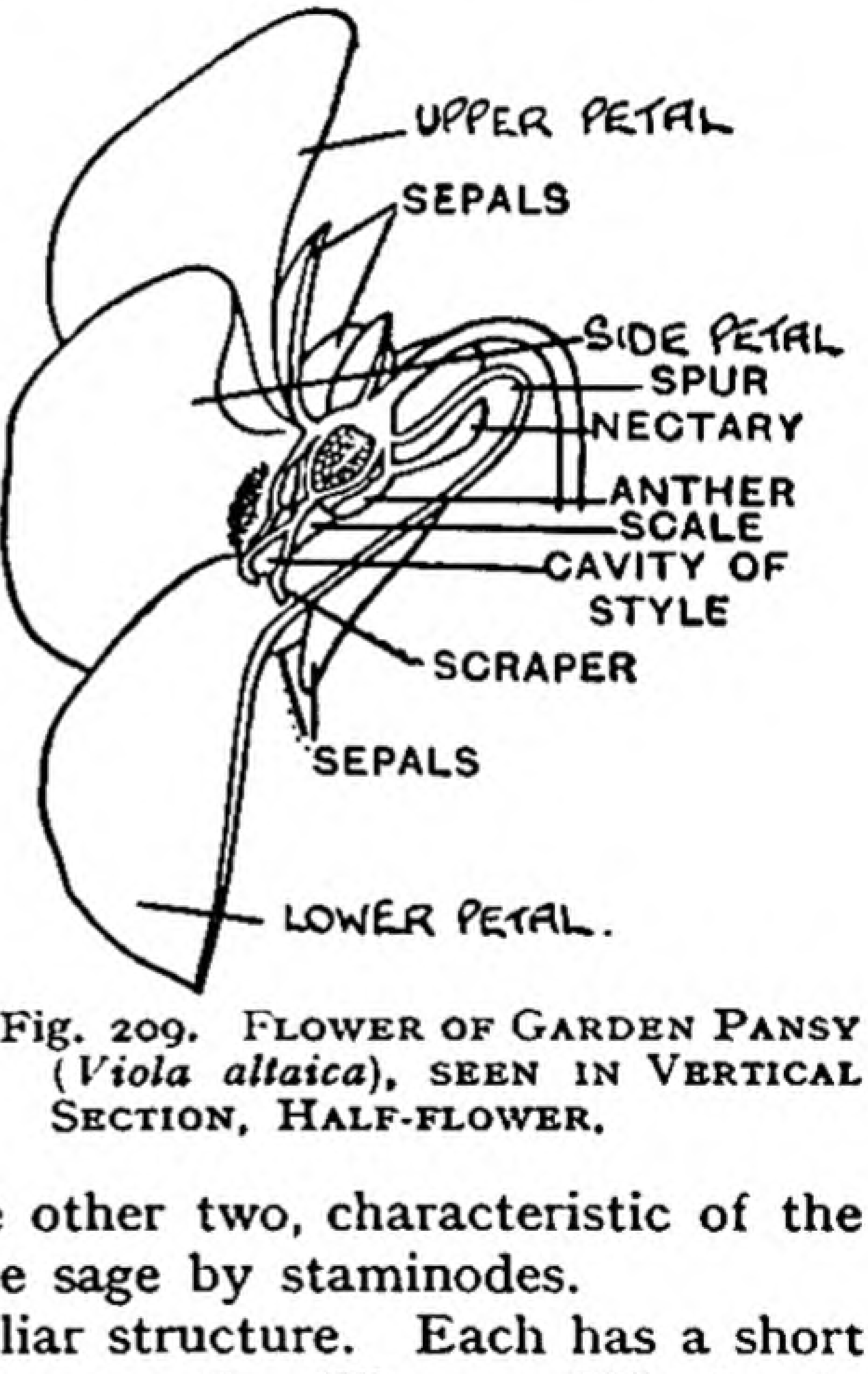


Fig. 209. Flower of Garden Pansy (*Viola altaica*), seen in Vertical Section, Half-flower.

The two stamens have a peculiar structure. Each has a short filament, jointed to a long curved connective (Fig. 210, III, *c*). In some types of *Salvia* each end of the connective bears a half-anther, but in other types (e.g. garden sage) the lower end of the connective is barren and flattened (Fig. 210, III, *b*), and the upper part of the connective is longer than the lower, the whole forming a delicate lever.

A bee on entering the flower pushes against the *united* lower ends of the two connectives in seeking the nectar, and causes the curved connectives to swing on the filaments as on hinges, so that the two fertile anther-lobes (*a*) come down and strike on the bee's back, dusting it with pollen. As the bee retires, the stamens return to their former place under the corolla-hood.

The flowers are protandrous. As the flower gets older the style curves down, and the stigma is so placed that it is touched by a bee entering the flower at this stage.

6. Special Arrangements for Self-pollination

In studying floral mechanisms we are too apt to forget that self-pollination occurs regularly in most flowers where it is not precluded by diœcism, complete dichogamy, or self-sterility. Many annual plants are commonly self-pollinated (e.g. groundsel, chickweed). They have small flowers, often without nectar or smell, and are either **homogamous,** that is, their anthers and stigmas mature at the same time, or so slightly dichogamous that self-pollination is secure.

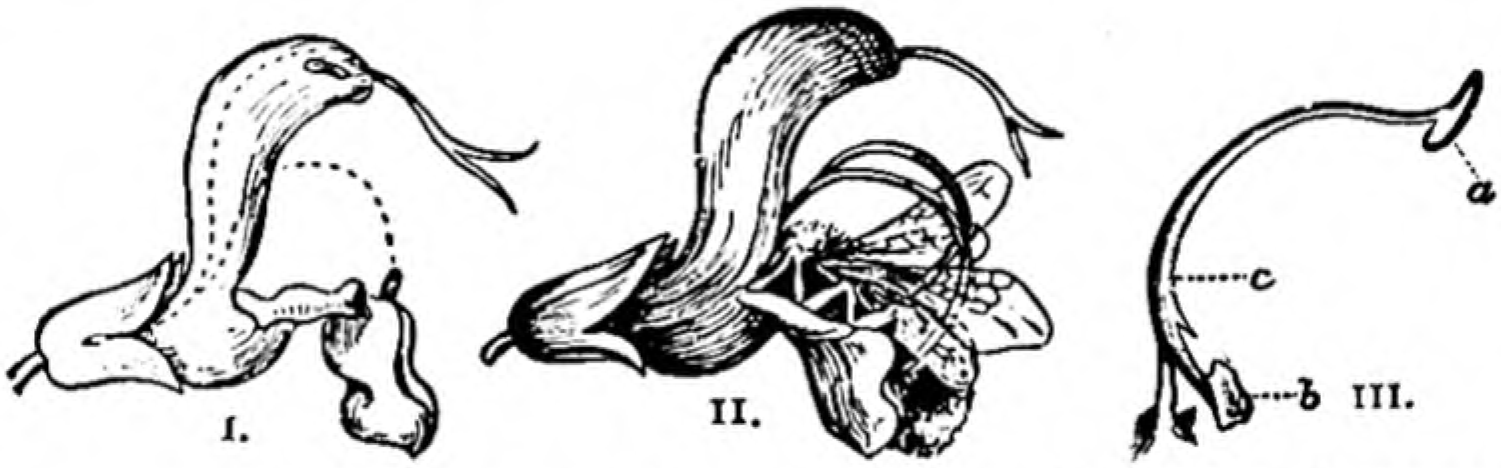


Fig. 210. I., Flower of *Salvia* from side; II., with Humble-bee extracting Nectar, and the Anthers rubbing against its Back; III., Single Stamen.

Even in flowers evidently adapted for cross-pollination, if this fails, there is commonly the possibility of self-pollination. Many of them are distinctly dichogamous, but not completely so, there being usually a short period during which self-pollination becomes possible. To effect this there are sometimes special contrivances such as the curling back of the stigmas to reach the pollen on the anthers or style (e.g. Compositae, Campanulaceae).

A very special adaptation for self-pollination is the production of **cleistogamous flowers.** These are closed flowers produced late in the year by certain plants which had previously produced entomophilous flowers, e.g. *Viola odorata, Oxalis acetosella, Lamium amplexicaule* (one of the deadnettles), etc. *Commelina benghalensis* also may produce cleistogamous flowers on leafless shoots. The cleistogamous flower is small and inconspicuous. The calyx remains closed, and the stamens and pistil are developed within it.

In *Viola odorata* the self-pollinating cleistogamous flowers have five very small petals and five stamens, but in the dog violet there are only two (anterior) stamens. The anthers produce few microspores, and do not open; the microspores germinate inside the anther, and the pollen-tubes (see § 8) grow through the anther-wall and the style to reach the ovules. The formation of these flowers is partly dependent on shade; they are always shaded by the leaves of the plant itself. If a plant is kept in feeble light, it will usually produce only cleistogamous flowers.

7. Protection of Pollen against Rain

Microspores are much less resistant to extremes of temperature and to drying when they have been moistened and in consequence have begun to germinate. Pollen may be protected from rain in various ways. In some flowers, especially those whose pollen is exposed to rain when the flower opens, the microspores are not readily wetted, having a covering of wax or of spines, etc.

Many flowers protect the pollen by their horizontal or drooping positon, e.g. Ericaceae, Liliaceae. In some cases the flower closes up at night or in bad weather, e.g. *Oxalis*, tulip, crocus, some Ranunculaceae; and the same kind of closing is effected in the capitula of many Compositae by the movement of the flowers and bracts (see p. 225). In iris the large petaloid stigmas cover the stamens (Fig. 228), and in many flowers the stamens are protected by a hood formed by the sepals or petals, or by both.

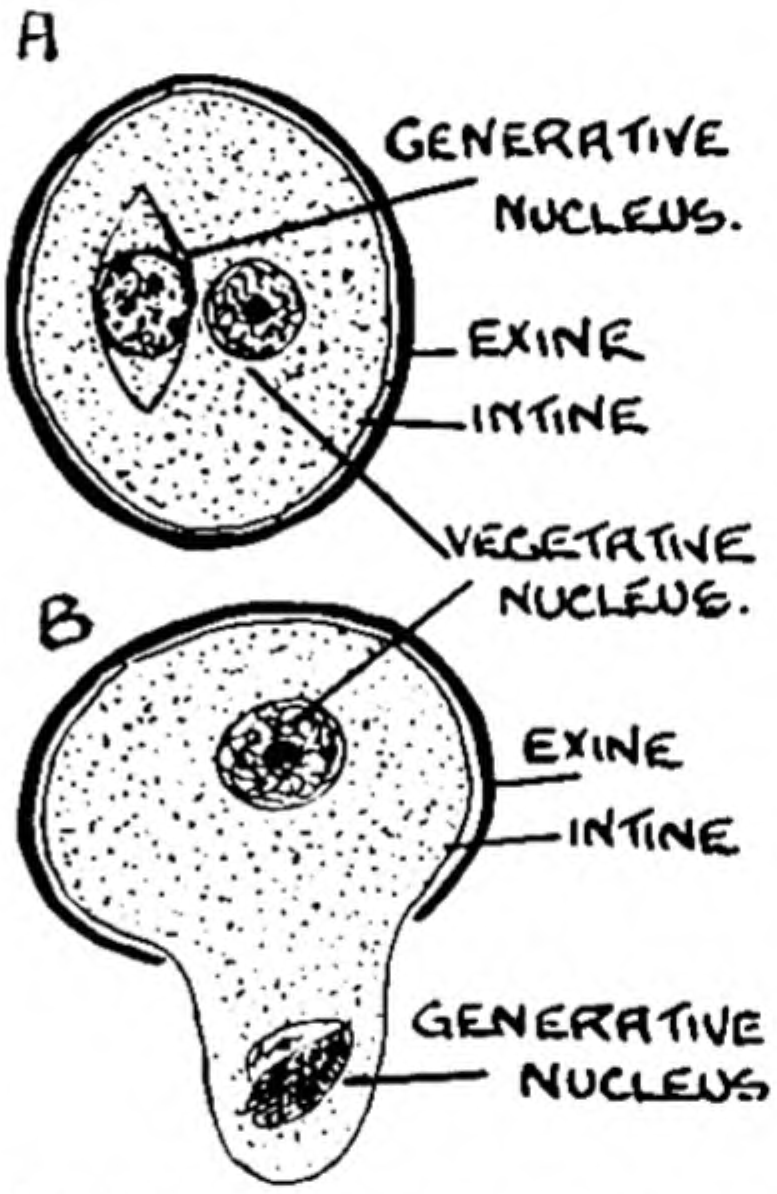


Fig. 211. A, Division of Microspore Nucleus; B, Germination of Microspore.

8. Germination of the Microspore.
Processes leading up to and ending in Fertilisation

At first the microspore is unicellular (Fig. 183), but later, even before it leaves the anther, its nucleus divides into two (Fig. 211, A). The larger one of these is the **vegetative** nucleus; the smaller one the **generative.** Both are free in the cytoplasm of the microspore. Either before or after pollination the generative nucleus divides into two **male gametes** (see p. 12). Germination and further development take place on the stigma, which secretes a sugary nutritive fluid.

From one of the pores in the exine a slender **pollen-tube** (Fig. 211, B) protrudes, and grows down through the tissue of stigma and style and finally enters the ovary. After entering the ovary the pollen-tube grows towards an ovule, which it enters usually by the micropyle. It penetrates the apex of the nucellus and comes in contact with the megaspore near to the oosphere and synergidae. During its growth the vegetative nucleus is found near the tip of the pollen-tube. The male gametes also pass down to the apex of the pollen-tube, but the vegetative nucleus is by this time disorganised. *One male gamete only* is concerned in the actual process of fertilisation. It passes from the pollen-tube into the megaspore and fuses with the oosphere or female gamete. The synergidae assist in the process, hence their names synergidae or " help-cells " (Gr. συν, with ϵργον, work). The tip of the pollen-tube swells and bursts, thus setting the male gametes free in the embryo-sac.

The fusion of the male gamete, which appears to be entirely nuclear, with the nucleus of the oosphere constitutes fertilisation in the strict sense. The fertilised oosphere secretes a cellulose wall and is then called the **oospore.** Its nucleus is diploid. The second male gamete fuses with the secondary nucleus of the megaspore. The resulting nucleus is called the *endosperm nucleus.* The significance of this process, which resembles fertilisation, and which, together with the actual fertilisation of the oosphere, constitutes what has been called "**double fertilisation,**" is considered in § 10.

In a few Dicotyledons, e.g. *Corylus* and *Betula*, the pollen-tube does not enter the ovule by the micropyle, but by piercing the chalaza. This is known as **chalazogamic** fertilisation as distinguished from the usual **porogamic** method.

9. Development of the Embryo

The act of fertilisation is followed by changes in the megaspore and ovary, and leads to the development of the seed and fruit. The embryo is developed from the oospore. After fertilisation the synergidae and antipodal cells disappear.

The development of the embryo in shepherd's purse (*Capsella Bursa-pastoris*) may be taken as fairly typical of Dicotyledons generally. The oospore first of all divides into a row of cells, the **pro-embryo.** Of these the cell farthest away from the micropyle, the embryonal cell, is mainly concerned with the production of the embryo; the remaining cells constitute the **suspensor.** The embryonal cell now divides by three walls at right angles into eight cells (octants). Four of these are posterior (next the suspensor), four anterior. This little mass of tissue is called the embryonal mass.

As the embryonal mass increases in size the various parts of the embryo are gradually differentiated. The *terminal* plumule and the two cotyledons are derived from the four anterior octants, the hypocotyl from the posterior octants; the growing point of the radicle is derived from the terminal cell of the suspensor, called the **hypophysis cell.** The marking out of plerome, etc., can be followed in Fig. 212.

In Monocotyledons, also, the division of the oospore gives rise to a pro-embryo; but the course of development differs in different groups, and there is no monocotyledonous plant in which the development of the embryo can be regarded as typical of Monocotyledons generally. In some cases no suspensor is formed and the whole of the embryo is developed from the embryonal cell. In other cases there is a filamentous suspensor which takes part to a greater or lesser extent in the formation of the embryo. This is the characteristic mode of development in monocotyledonous aquatic plants of which *Alisma plantago* may be taken as an example (Fig. 213). In members of the Liliiflorae the greater part of the embryo is developed from the embryonal mass, and consists mainly of cotyledon tissue enclosing, near its base, the rudimentary plumule. The persistent suspensor cells give origin to the root-cap and piliferous layer.

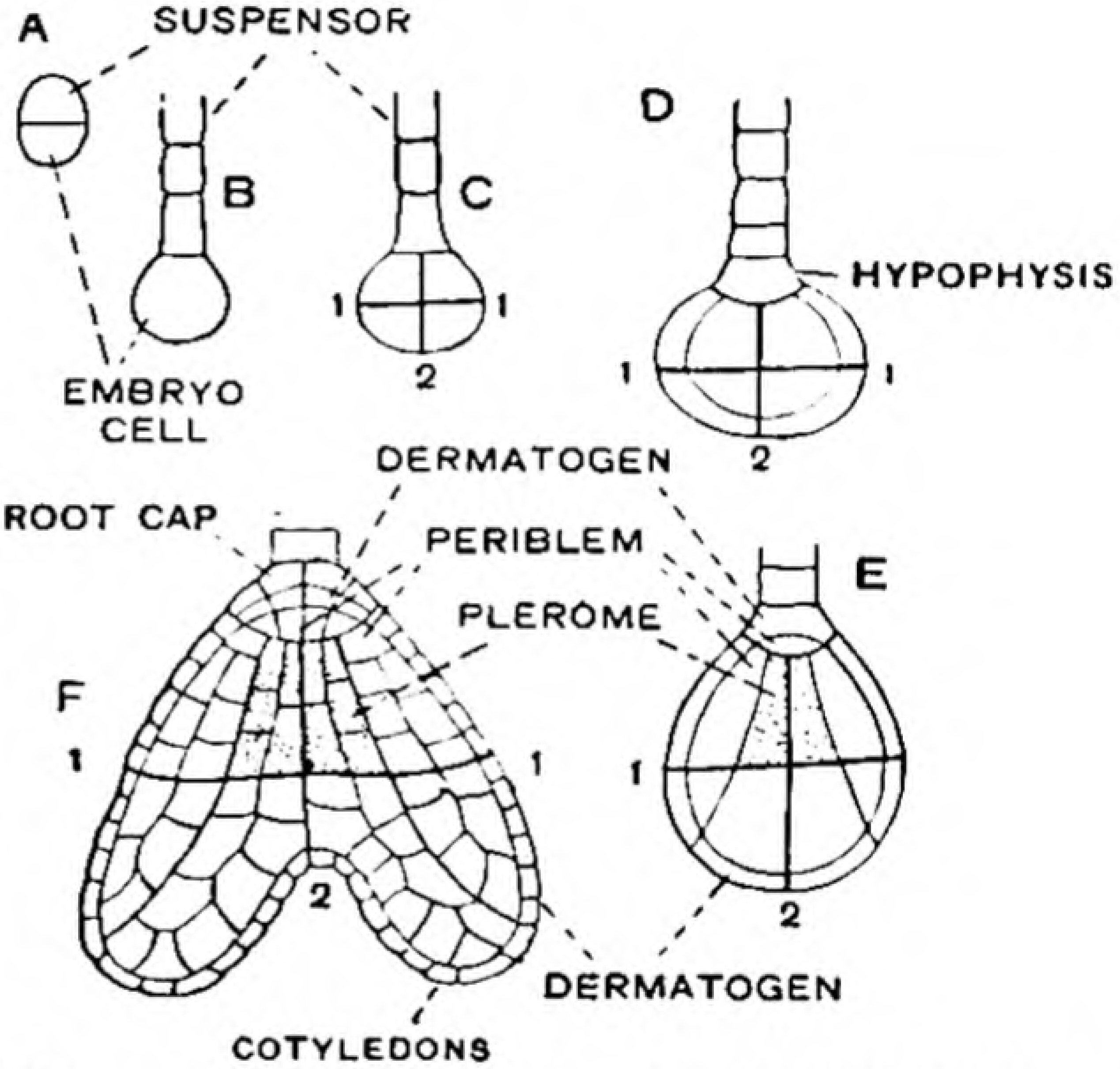


Fig. 212. Development of Dicotyledonous Embryo (*Capsella Bursa-pastoris*, the Shepherd's Purse).

A, First division of oospore. Only two of the octant-walls (1, 2) can be shown.

The chief point to notice in the development of the monocotyledonous embryo is that, except in a very few cases, the cotyledon is a *terminal* structure, and the plumule arises lateral to it.

In some plants, e.g. orchids and most parasitic plants, the embryo consists of an undifferentiated mass of cells when the seed enters on its resting stage.

The Suspensor. The main function of the suspensor appears to be to push the developing embryo well into the embryonic sac where it is surrounded, at least in the early stages, by the developing endosperm. Occasionally, however, the suspensor acts as an absorbing organ for the embryo, and sends out processes like haustoria which penetrate the nucellus, integuments and placenta and take up food materials (e.g. some orchids).

10. Development of the Endosperm

While the segmentation of the oospore and the development of the embryo are taking place other changes are proceeding in the megaspore. The endosperm nucleus begins rapid mitotic division. Each mitosis may be followed by cell-wall formation, or a large number of small nuclei may first be formed and become embedded in the cytoplasm of the megaspore (free nuclear division). Cytoplasm aggregates round these nuclei to form protoplasts (p. 15), and finally cell-walls may be laid down between them. Thus from the endosperm nucleus, a tissue is formed in the megaspore. The cells of this tissue become filled with food-material (starch, oil, aleurone grains, etc.) built up from soluble compounds which diffuse into them from the placenta. The nutritive tissue thus formed in the megaspore is the **endosperm.** A few seeds possess a *ruminate* endosperm, due to the infolding of the nucellus tissue (*i.e.* perisperm, as in *Myristica*) or of the testa (as in areca nut) into the endosperm during development, producing a mottled appearance when seen in section.

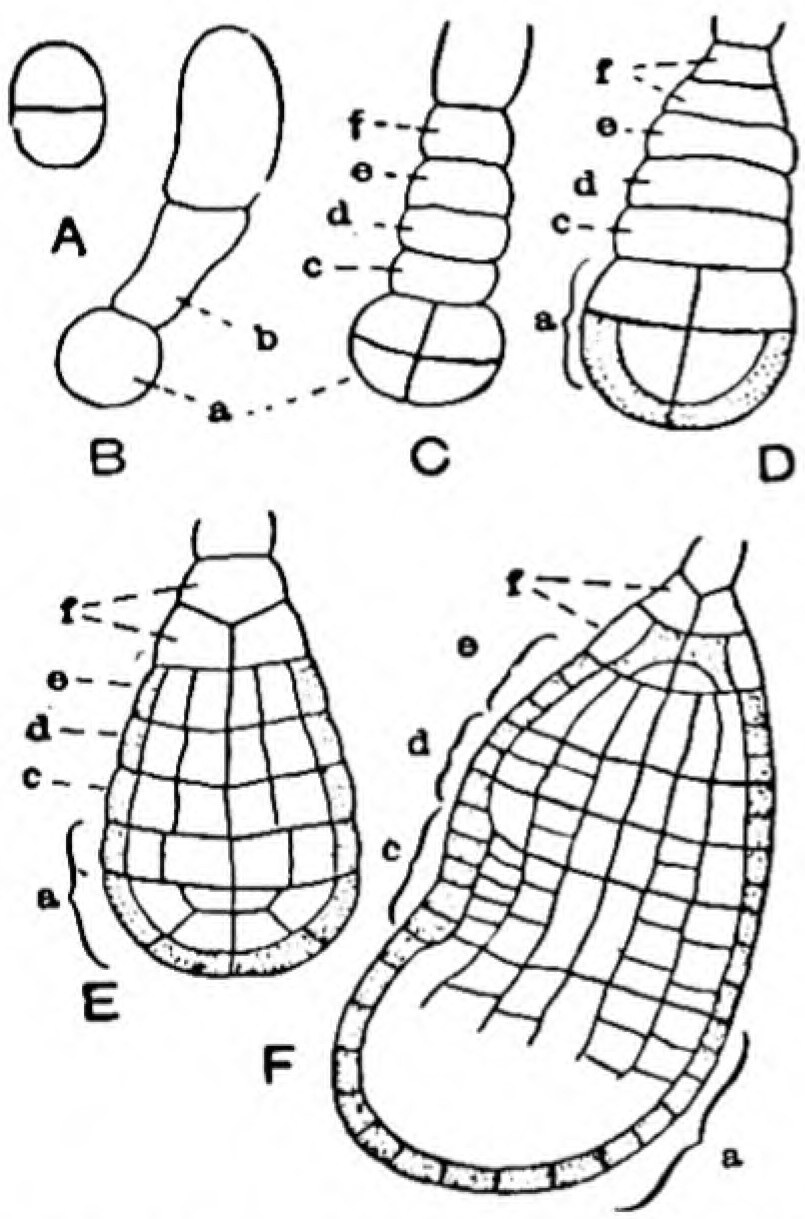


Fig. 213. DEVELOPMENT OF MONOCOTYLEDONOUS EMBRYO (*Alisma*).

a is the Embryonal Cell (in B) forming the embryonal mass (in C, D, E, F); it gives rise to the cotyledon. *c, d, e, f* are formed by division of *b*, the terminal cell of suspensor. *c* gives growing-point of stem; *d, e* give hypocotyl, *f*, the growing-point of root.

11. Parthenogenesis, Apogamy and Apospory

In a few Angiosperms (e.g. *Thalictrum, Alchemilla, Taraxacum, Hieracium,* etc.), embryos may develop from "egg-cells," which have not been, and, indeed, are incapable of being fertilised. These "egg-cells" are not normal female gametes, but have nuclei similar to those of normal vegetative cells (*i.e.* are diploid). This phenomenon, the development of an embryo from an unfertilised "egg-cell," is called *parthenogenesis.* On the other hand, cells of a normal megaspore, such as antipodal cells or synergidae, may, under certain circumstances, produce an embryo. Cells of the nucellus may do likewise. These are two forms of *apogamy*, *i.e.* the production of embryos without the fusion of gametes. Further, the tissue of the ovule immediately external to the nucellus, *i.e.* the integument, may develop an enlarged cell which replaces the true megaspore, and develops an embryo without fertilisation. This formation of an embryo in a cell which is not a true spore is known as *apospory*.

12. Polyembryony

In some plants a number of embryos may be formed in one ovule, and be found in the resulting seed. This phenomenon is known as *polyembryony*. It may be due to the presence of more than one megaspore in the same ovule, or of more than one oosphere in a megaspore. It may also be due to the division of the oospore into more than one pro-embryo (e.g. *Pinus*).

13. Formation of Seed

Along with the development of the embryo and endosperm, and the consequent enlargement of the megaspore, other changes occur in the tissues external to it. The nucellus usually becomes disorganised and practically disappears, but in a few cases it becomes either an accessory, or even the main, storage tissue, quite distinct from the endosperm, and external to it, called the **perisperm.** Examples of perisperm are seen in pepper, cardamom and water lily. The integuments become the protective covering, the outer integument forms the testa, the inner, the tegmen. The micropyle persists as a pore, the funicle forms the raphe, and its scar the hilum. Thus we have a typical *endospermous seed*. In the *non-endospermous* type, endosperm is present in the early stages of development, but is absorbed as the embryo grows and comes to fill the megaspore.

14. Aril and Caruncle

Sometimes *after fertilisation* an additional investment grows up around the testa from the placenta, funicle or micropyle. It is usually fleshy, but may have other forms, and all are different kinds of *aril* or *arillus*. In the spindle-tree (*Euonymus*) it is fleshy and micropylar in origin; in the Dilleniaceae it is funicular. The mace of the nutmeg (*Myristica*) is an aril developed from funicle and micropyle. Smaller, fleshy growths of the seed are called *caruncles*; in pansy (*Viola*) it is formed at the hilum, in castor-oil (*Ricinus*) and spurge (*Euphorbia*) at the micropyle. The tuft of hairs on the seed of willow-herb (*Epilobium*) is also of this nature. The term *strophiole* is applied to a somewhat fleshy structure formed from the funicle and present as an appendage to the hilum of the seed as in *Datura fastuosa*. *Colchicum autumnale* has a thickened funicle of similar nature.

CHAPTER XII

FRUITS AND SEEDS

1. The **fruit** of the Angiosperm in the wide sense is the entire result of secondary growth induced in the ovary and neighbouring parts of the flower by the stimulus of fertilisation. It usually consists of the ripened ovary only, but frequently other parts of the flower take a share in the formation of the fruit, e.g. the receptacle, or the perianth-leaves. The wall of the ovary becomes the **pericarp** or fruit-wall, which may either remain soft and fleshy, or become dry and hard.

Distinctions have been made between *true fruits*, formed from the ovary alone, and *false fruits* (*pseudocarps*), in the formation of which other parts of the flower share. No great importance can be attached to this distinction. It would lead, for example, to the view that all fruits formed from inferior ovaries are false fruits, seeing that in the inferior ovary the carpels are adherent to the receptacle. The really important thing in connexion with the study of fruits is to interpret the manifold peculiarities of form and structure which they exhibit and relate these to the functions of seed-protection and seed-dispersal.

2. Classification of Fruits

Fruits may be **simple, aggregate,** or **composite.** A *simple fruit* is one which is formed from a *single* flower in which the pistil is monocarpellary or syncarpous, e.g. the pod of pea, the capsule of poppy. An *aggregate fruit* is one which is formed from a *single* flower in which the gynaeceum is apocarpous. Here each carpel (or rather ovary) gives rise to a fruitlet, and the fruit therefore consists of an aggregation of fruitlets. A *composite fruit*, on the other hand, is formed from an *inflorescence*, not from a single flower. Here all the flowers increase in size, become aggregated together, and form a single mass. These composite fruits are called *syncarps*.

The **simple fruits** are further subdivided into **dry** and **succulent** according as the pericarp is dry and firm or more or less fleshy and juicy. The *dry simple* fruits are either **achenial, capsular,** or **schizocarpic**; the *succulent simple* fruits may be **drupaceous, baccate,** or **pomes.** The *aggregate fruits* are collections of one or other of these simple forms. The *syncarps* have peculiarities which distinguish them from the others.

It should be noticed that there is no sharp distinction between dry and succulent fruits. There are examples of fleshy capsules and dry drupes.

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3. Achenial Fruits

Achenial fruits may be defined as *dry, indehiscent, one-seeded,* fruits. The term indehiscent means that the pericarp does not naturally open to allow the seed to escape. The pericarp and testa are both ruptured when the embryo begins to develop at germination. The chief types of achenial fruits are:—

(*a*) The **achene.** In this the pericarp is membranous or leathery. It is formed from a superior ovary, and pericarp and testa are free from each other. Examples are found in the Polygonaceae (dock and sorrel). Many aggregate fruits consist of collections of achenes (e.g. Ranunculaceae).

(*b*) The **cypsela** (Figs. 38 and 214, A). This differs from the achene only in being developed from an inferior ovary. It is the characteristic fruit of the Compositae (sunflower, daisy, etc.). In many cases it is crowned by a persistent hairy *pappus* (p. 236) which serves to disseminate the fruits (e.g. dandelion, thistle, groundsel, etc.).

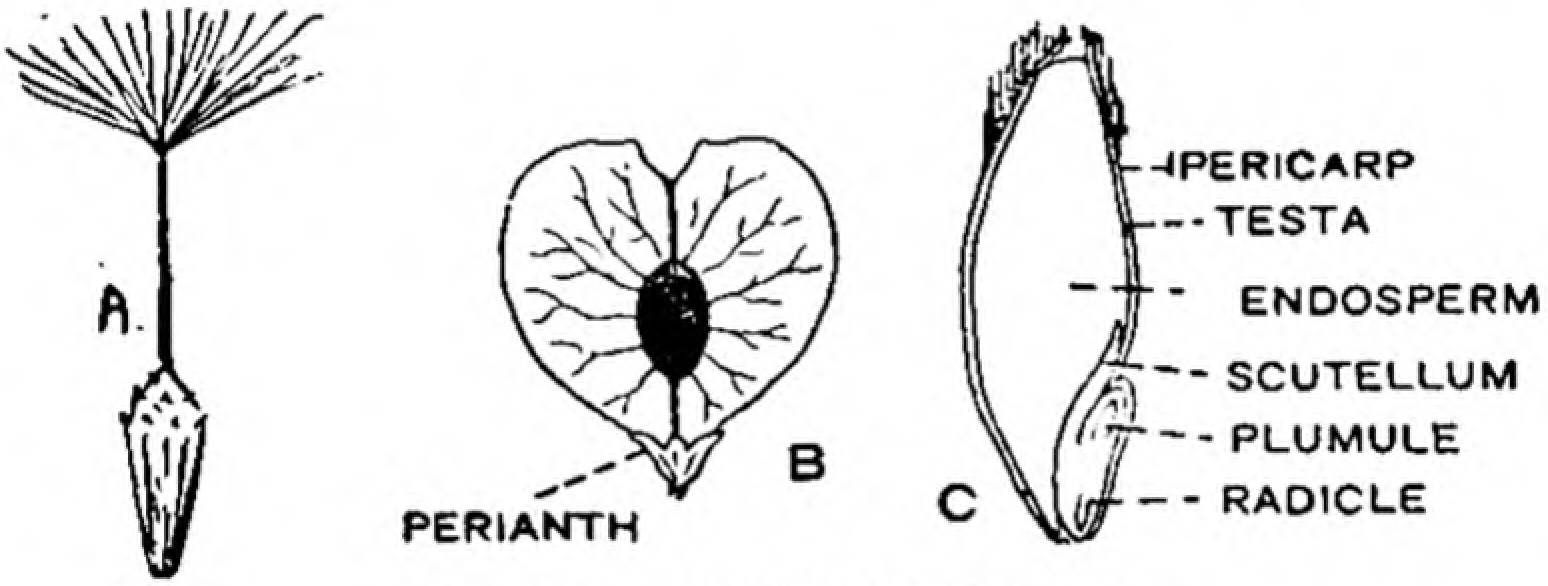


Fig. 214. ACHENIAL FRUITS.

A, Cypsela of Dandelion, with pappus; B, Samara of Elm; C, Caryopsis of Oat, removed from husk, seen in longitudinal section.

(*c*) The **caryopsis** (Figs. 41 and 214, C). This is an achene in which the pericarp and testa are fused together. It is the characteristic fruit of grasses (oat, maize, barley, etc.). In many cases the fruit or "grain" is invested by the persistent bract and bracteole (e.g. oat).

(*d*) The **samara,** or *winged* achene. Here the pericarp has developed a membrane or wing which plays an important part in the dispersal of the fruit, e.g. ash (Fig. 44) and elm (Fig. 214, B).

(*e*) The **nut.** In this the pericarp is hard and woody, forming a shell. The term is usually applied to all large or hard-coated achenes. Typical examples are found in hazel (Fig. 241), oak (Fig. 42), beech, sweet chestnut. In these examples the nuts are invested by a hard or membranous structure called the **cupule**, derived from the fusion of bracteoles developed beneath the flower. Sometimes the cupule encloses one nut, sometimes several. The cup or cupule of the acorn and the membranous "husk" of the hazel-nut are well known. In sweet chestnut two nuts are enclosed in a spiny cupule, and in beech there are usually two triangular nuts enclosed in a cupule which is almost closed and also slightly spiny.

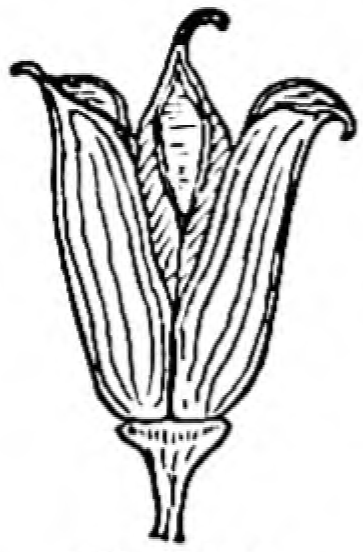


Fig. 215. COLLECTION (ETAERIO) OF FOLLICLES OF MONKSHOOD.

It is important to distinguish these cupules from the capsules presently to be described. Many structures, popularly called nuts because they have a hard shell, are not really nuts. Thus the "brazil-nut" is a seed (derived from a capsular fruit). The walnut is part of a drupaceous fruit (p. 285).

4. Capsular Fruits

These are *dry, dehiscent, many-seeded* fruits. The term dehiscent means the fruits break open naturally to allow the seeds to escape. There are different kinds of capsular fruits:—

(*a*) The **follicle** is formed from the ovary of a single carpel. It splits open along one side only, usually the ventral suture (p. 246). There is no common example of the simple follicle; but many aggregate fruits consist of collections of follicles (Figs. 176, 215, and see Ranunculaceae).

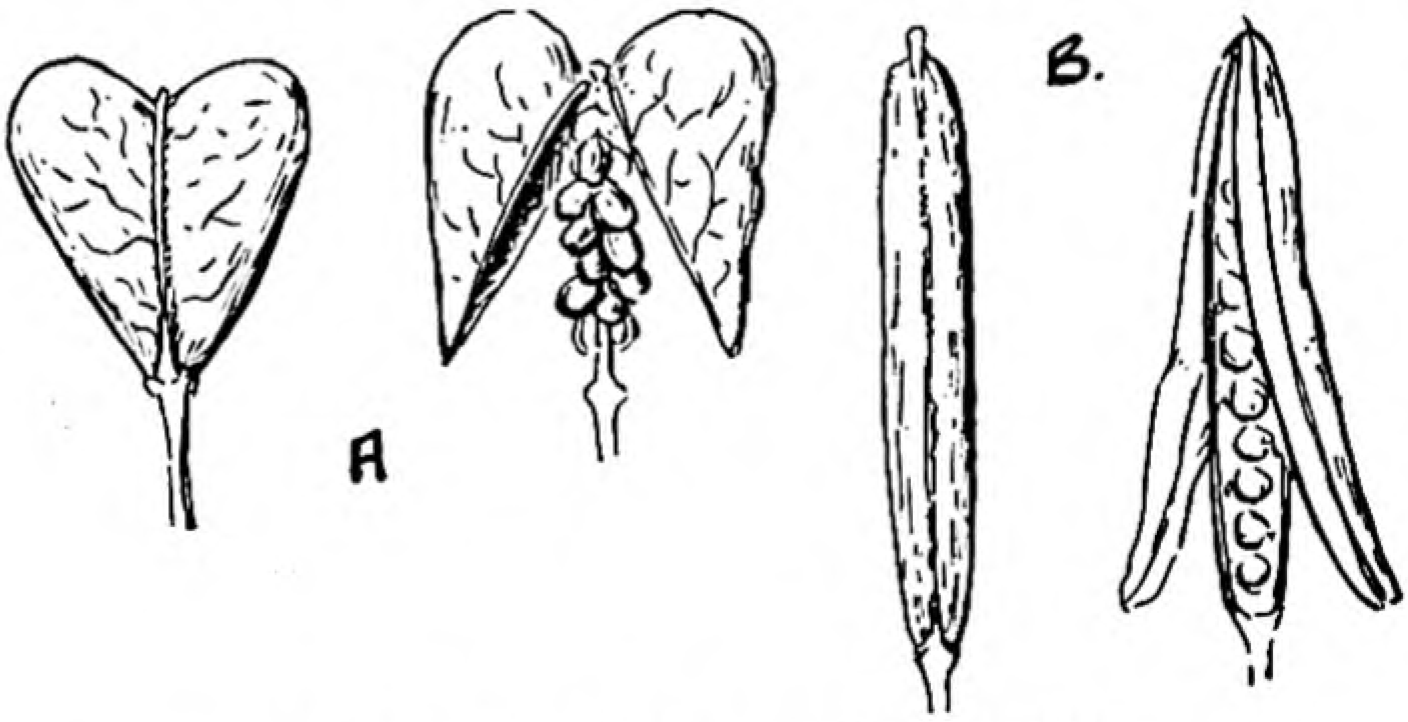


Fig. 216. FRUITS OF CRUCIFERAE.

A, Silicula of shepherd's purse; B, Siliqua of wallflower.

(*b*) The **legume** or *pod* is formed from the ovary of a monocarpellary pistil (Fig. 184). It differs from the follicle in dehiscing along both dorsal and ventral sutures. It is the characteristic fruit of the Papilionatae (pea, bean, etc., Fig. 222, A).

(*c*) The **siliqua** is a characteristic fruit of the Cruciferae, e.g. *Nasturtium*, *Brassica*, *Cardamine* and *Eruca*. It is developed from a bilocular ovary with two parietal placentas and a *false* septum stretching between them. It is a long, cylindrical fruit, and, in dehiscing, the two walls of the loculi break away from the two placentas and false septum, and hang freely suspended from the apex of the fruit (Fig. 216, B). Thus the two placentas are left behind, forming a two-ribbed framework called the **replum**, across which the false septum stretches. The seeds are, of course, exposed on this structure.

(*d*) The **silicula** (Fig. 216, A) is a short, flat form of siliqua (e.g. *Capsella*, *Lepidium* and *Senebiera*).

(*e*) The **capsule** includes all other forms of capsular fruits. Capsules are formed from polycarpellary, syncarpous pistils, and may be unilocular or multilocular. Occasionally they are not dry, but more or less fleshy, e.g. in *Aesculus*, *Impatiens*, and *Oxalis*. Various modes of dehiscence are met with. In *porous dehiscence* the seeds escape through little holes or pores in the wall of the capsule, either at the apex (e.g. *Linaria*, *Papaver*, Fig. 217) or at the base (e.g. *Campanula*). The capsule of *Stellaria* and other Caryophyllaceae splits about halfway down (Fig. 222, B) often into twice as many teeth as there are carpels (*dehiscence by teeth*). In *Plantago*, *Anagallis* and *Hyoscyamus* there is transverse dehiscence, leading to the separation of a lid from the top of the capsule. Such a capsule is called a **pyxidium** (Fig. 277, A). Usually, however, capsules open longitudinally, either along the midribs of the carpels (dorsal sutures) as in some Liliaceae, Amaryllidaceae, Iridaceae and Scrophulariaceae, or along the septa between the loculi of the ovary, as in some Liliaceae. The segments into which the ovary splits are sometimes referred to as *valves*.

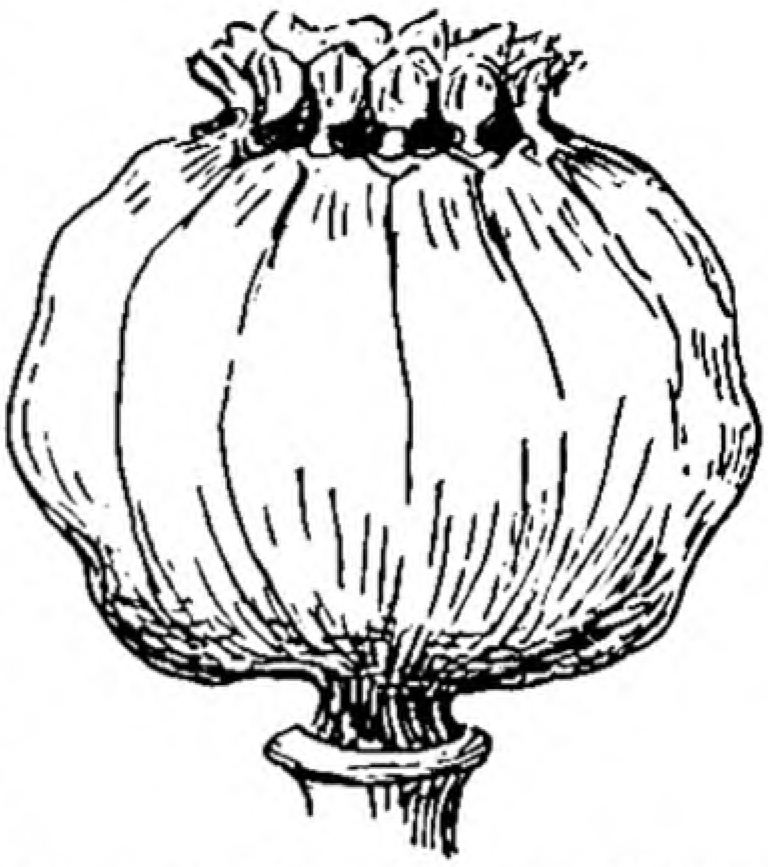


Fig. 217. CAPSULE OF POPPY SHOWING PORICIDAL DEHISCENCE.

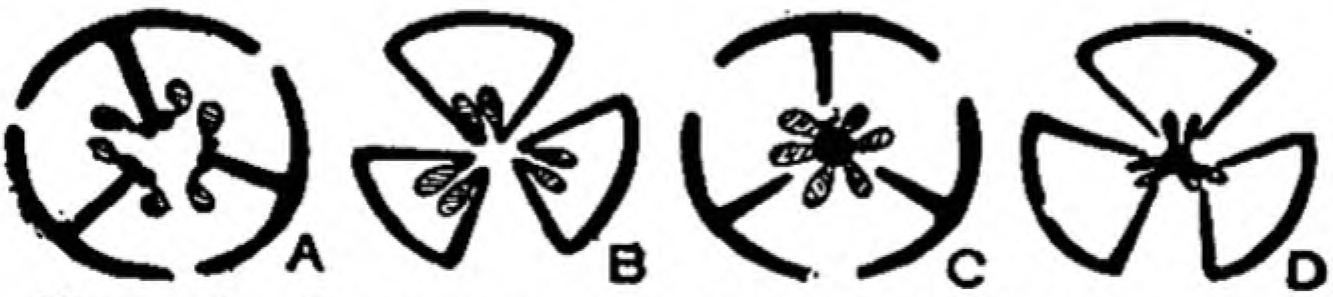


Fig. 218. DEHISCENCE OF MULTILOCULAR CAPSULES.
A, Loculicidal; B, Septicidal; C and D, Septifragal.
(Diagrammatic transverse sections.)

In *multilocular capsules*, with axile placentation, the dehiscence is *loculicidal* (Fig. 218, A) if the slits run down the middle of the carpels (*i.e.* open into the loculi), the *septa and placentas* breaking away down the centre of the fruit (*Iris*); *septicidal*, if the slits run down the middle of the septa, the placentas separating along their line of junction (*Rhododendron*); *septifragal*, if the slits appear as in loculicidal or septicidal dehiscence but the septa break away from the placentas and leave the latter and the seeds in the middle of the fruit (e.g. *Datura*, thorn-apple, Fig. 277, C).

5. Schizocarpic Fruits (Schizocarps)

These are dry, many-seeded fruits, which, as they ripen, *split up* into a number of one-seeded and usually indehiscent parts resembling achenes and called **mericarps.** The best known are:—

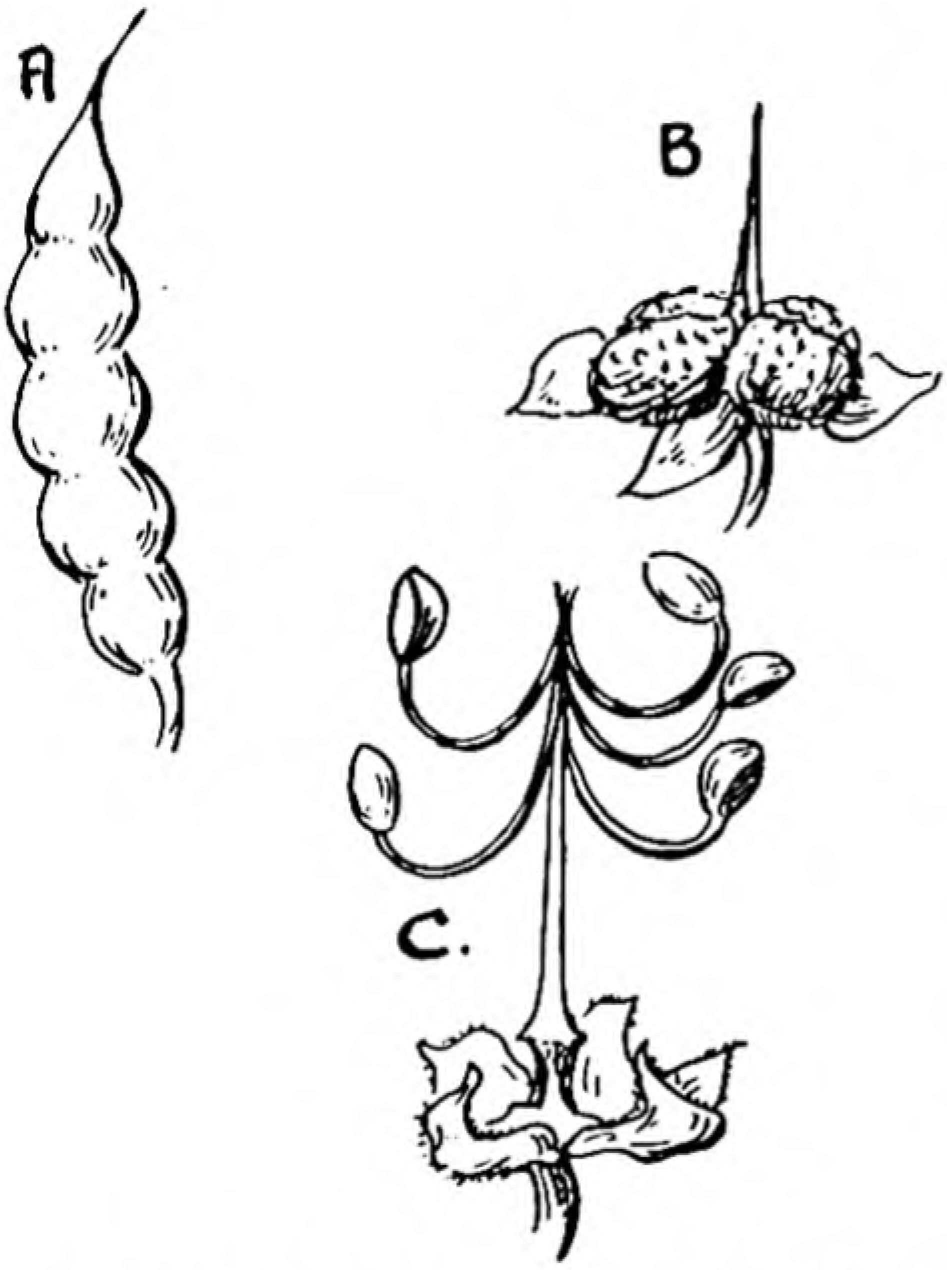


Fig. 219. SCHIZOCARPIC FRUITS.

A, Lomentum of *Hedysarum*; B, Carcerulus of *Cynoglossum*; C, Regma of *Geranium*.

(*a*) The **Lomentum.**—This is found in some Papilionatae (e.g. *Hedysarum*, Fig. 219, A), *Arachis*, *Desmodium*, and some Cruciferae (e.g. *Raphanus*), in which the fruit (pod or siliqua) is constricted between the seeds and splits *transversely* at the constrictions into one-seeded pieces. More correctly the fruit is described as a lomentaceous pod or siliqua, as the case may be.

(*b*) The **Cremocarp** (Fig. 220, A, B).—This is the characteristic fruit of the Umbelliferae. It is developed from a bicarpellary pistil with a bilocular, inferior ovary in each loculus of which there is a single suspended ovule (Fig. 188). As it ripens the cremocarp splits *longitudinally* (between the two loculi) into two mericarps, which are indehiscent and remain for some time attached by the stylopod to a central axis called the *carpophore*. Each mericarp contains a seed. These mericarps are *popularly* called seeds, e.g. caraway "seed" (Fig. 220).

(*c*) The **Carcerulus** (Figs. 219, B and 266).—This is the characteristic fruit of the families Labiatae and Boraginaceae. In these families the fruit is formed from a bicarpellary pistil with a *superior* ovary which becomes quadrilocular owing to the formation of two false septa. As the fruit ripens the four mericarps separate from each other towards the middle. In the carcerulus of *Malva* the *superior* ovary of the polycarpellary pistil splits into a large number of mericarps.

(*d*) The **Regma** (Fig. 219, C).—This is a schizocarp which breaks up into one-seeded *dehiscent* parts, each of which is called a *coccus*, e.g. geranium and castor-oil fruits. In geranium the pistil is formed of five carpels fused round the base of a long carpophore. The five styles of the carpels are also adherent to the carpophore. When ripe the cocci break away and remain suspended by their styles from the apex of the carpophore.

(*e*) The **Double Samara.**—This is seen in *Acer* sp. and Sapindaceae where it may consist of two, three or four samaras.

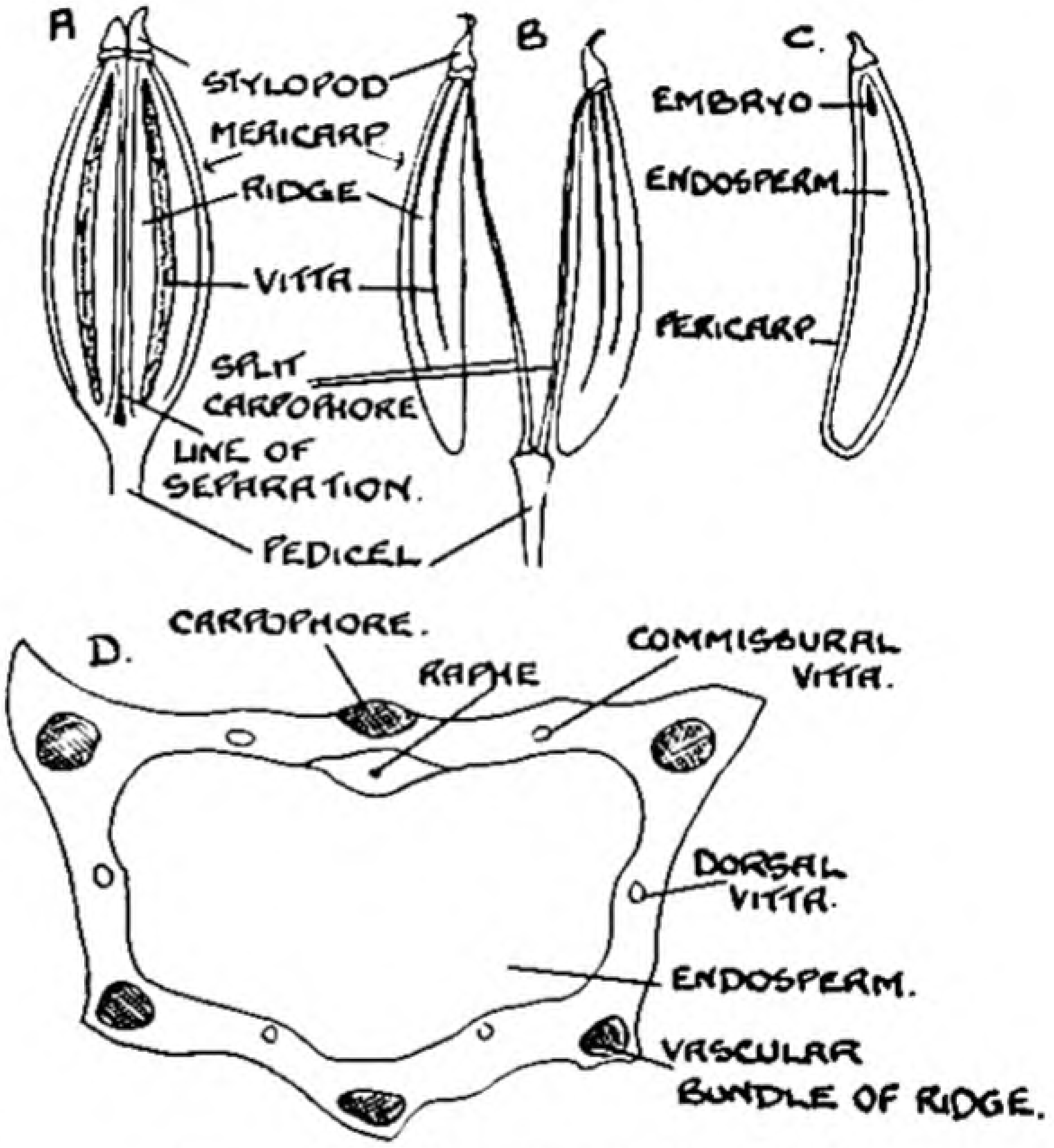

A
B
C.
STYLOPOD
MERICARP
RIDGE
VITTA
SPLIT CARPOPHORE
LINE OF SEPARATION.
PEDICEL
EMBRYO
ENDOSPERM
PERICARP
D.
CARPOPHORE.
RAPHE
COMMISSURAL VITTA.
DORSAL VITTA.
ENDOSPERM.
VASCULAR BUNDLE OF RIDGE.

Fig. 220. FRUIT OF *Fœniculum*.

A, External; B, Mericarps separated; C, Mericarp in L.S.; D, Mericarp in T.S.

6. Drupes ("Stone" Fruits)

A simple drupe, e.g. cherry, apricot, mango, etc., is formed from a monocarpellary pistil with a superior ovary (Fig. 174, D). The pericarp shows three regions: (*a*) the *epicarp* or outer skin, (*b*) the *mesocarp* or middle fleshy region, and (*c*) the *endocarp*, the hard inner part, forming the "stone," which encloses and protects the seed. Usually there is only one seed (Fig. 257, E).

The drupe of almond has a velvety skin and rather tough mesocarp, which splits along one side; the shell (endocarp) has sometimes two seeds inside it.

Drupes may, however, be syncarpous, in which case each chamber of the ovary may form a distinct stone. Examples of such compound drupes are seen in the section Rutoideae of the Rutaceae. The walnut and coconut are drupes formed from syncarpous pistils.

The thin mesocarp of the walnut peels off during ripening, and allows the " stone," enclosing a single seed, to escape. The cartilaginous partitions passing in between the cotyledons (which are covered by the testa) are ingrowths from the endocarp.

In the coconut the mesocarp (removed before export) is fibrous. Hence the fruit has been called a " fibrous drupe." The shell is the endocarp; the edible substance is the endosperm; and the brown layer covering it the testa. A minute monocotyledonous embryo is embedded in the endosperm at one end (below one of the three pits at the broader end of the " nut "). There is a cavity in the middle of the endosperm filled with sap (so-called " milk ").

7. Baccate Fruits, or Berries

These are succulent fruits in which the succulent mass is more or less pulpy, and the seeds, which are usually hard, are embedded in the pulp. The berry differs from the drupe essentially in the fact that there is no stony endocarp, although epicarp, mesocarp, and endocarp may be differentiated. Baccate fruits may be derived from inferior (e.g. *Agave*, *Musa*, *Ribes*, pomegranate, melon, cucumber), or from superior ovaries (e.g. grape, orange, papaw).

The orange is a multilocular superior berry with axile placentation; the outer glandular skin is the epicarp, the underlying white substance the mesocarp, and the inner membrane lining the loculi the endocarp. The juice is contained in a large number of multi-cellular hairs developed from the walls of and filling the loculi.

In gooseberry and pomegranate the pulp, or edible portion of the berry, is derived largely (gooseberry) or entirely (pomegranate) from the outer coats of the seeds.

The date is a berry and not a drupe; the " stone " is not endocarp but seed (Fig. 46). The outer skin of the date is the epicarp; the sticky mass underneath, the mesocarp. Surrounding the stone is a thin membranous endocarp. The banana is a berry which rarely produces seed. The fruit of the Cactaceae is a berry derived from a unilocular inferior ovary.

8. The Pome

This is the fruit of the apple, pear, and some other Rosaceae. We may take the apple as an example. In the flower of the apple there are five imperfectly fused carpels enclosed in a hollow receptacle (Fig. 174, F). This is an extreme form of perigyny. As development proceeds, however, the carpels become adherent to the receptacle so as to produce the epigynous condition. The whole fused mass forms the pome (Fig. 257, A). The outer skin and the fleshy part of the apple are formed from the receptacle. The cartilaginous central part (core) is derived mainly from the carpels and is therefore the pericarp containing the seeds. The term epicarp, mesocarp, and endocarp should not be used for these three regions of the fruit.

Pomes are also found in quince (*Cydonia*), medlar (*Mespilus*) and *Cotoneaster*.

9. Aggregate Fruits

The aggregates of simple fruitlets are called " **etaerios.**" There may be etaerios of achenes, follicles, or drupes:—

(*a*) A typical etaerio of achenes is found in *Ranunculus* (Fig. 172) and other members of the Ranunculaceae, e.g. *Thalictrum, Anemone, Naravelia* and *Clematis*. In the last two genera the styles are persistent and become hairy. Similar etaerios are present in certain of the Rosaceae, e.g. *Potentilla* and *Alchemilla*. In *Fragaria* the achenes are distributed over the surface of an enlarged, fleshy receptacle (Fig. 257, C). In *Rosa* they are enclosed in a persistent hollow receptacle which becomes somewhat fleshy.

(*b*) Etaerios of follicles (Fig. 215) are found in some Ranunculaceae, e.g. *Aconitum, Delphinium, Helleborus*; some Apocynaceae, e.g. *Strophanthus, Lochnera, Alstonia*; and some Crassulaceae, e.g. *Kalanchoe*.

(*c*) Etaerios of drupes are seen in *Rubus* species (Fig. 257). The little drupes, derived from the separate carpels, are inserted on a conical receptacle.

10. Composite Fruits

These are not numerous; good examples are the fruits of the fig, jak, pineapple, mulberry, and hop.

(*a*) The **Fig.**—Here the inflorescence is a peculiar hollow, pear-shaped form of capitulum, the flowers being developed inside (Fig. 221, A). These flowers are pistillate and are pollinated by a species of wasp from the staminate flowers of the wild fig (caprification). As the fruit ripens, the inflorescence axis becomes fleshy and rich in dextrose. The true fruits are drupes, developed from the ovaries of the numerous small flowers. The "seeds" found in ripe figs are the true seeds invested by the hard endocarp. This composite fruit is called a **syconus.**

(*b*) **Pineapple** and **Mulberry.**—Here the composite fruit is called a **sorosis.** It is formed from a spike. In *pineapple* the fleshy axis and the flowers all fuse together. The areas on the surface of the fruit represent the flowers. Seeds are rarely formed. Above the flowers the axis produces a number of leaves forming the " crown." In *mulberry* (Fig. 221, B) the perianths in the female spike become fleshy, and enclose the true fruits. Jak and breadfruit are also the products of inflorescences in which the perianth and axis become fleshy and surround the individual achene-like fruits.

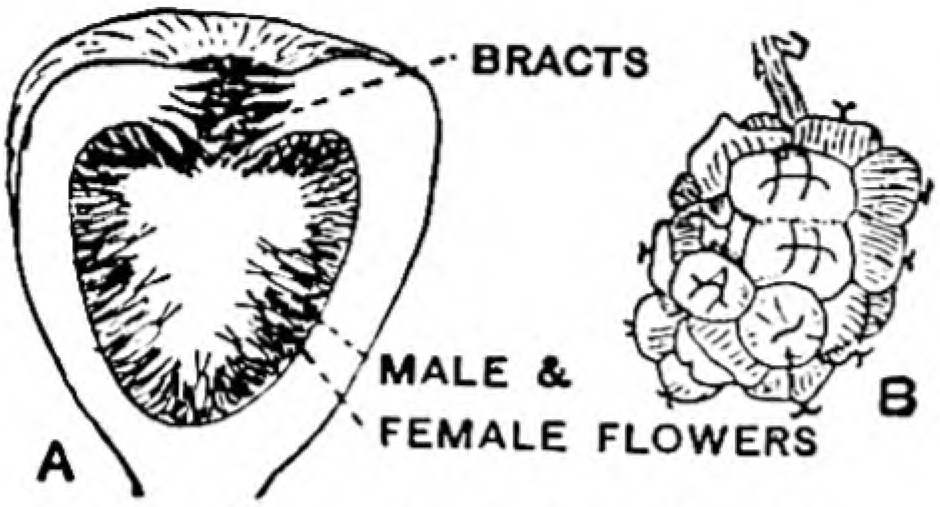


Fig. 221. Composite Fruits.

A, Fig, syconus cut longitudinally; B, Mulberry, external.

(*c*) The **Hop.**—Here the composite fruit develops from an inflorescence consisting of an axis bearing a number of membranous scales. These scales represent fused pairs of stipules belonging to bracts which themselves are suppressed. In the axil of each scale are two pistillate flowers, each flower enclosed in a bracteole (Fig. 221, C). These latter, after fertilisation of the flowers, enlarge and project beyond the scales. The whole inflorescence becomes a cone-like **strobilus.** The true fruits are achenes, enfolded in their bracts.

There are some fruits which it is difficult to classify. For example, the " berry " of some Araliaceae, e.g. *Aralia, Polyscias* and *Hedera* (ivy) is a fleshy fruit containing several seeds; these are not enclosed in a stony endocarp, but there is a firm investment round each. The fruit, to some extent, resembles a drupe, and may be called a drupaceous berry.

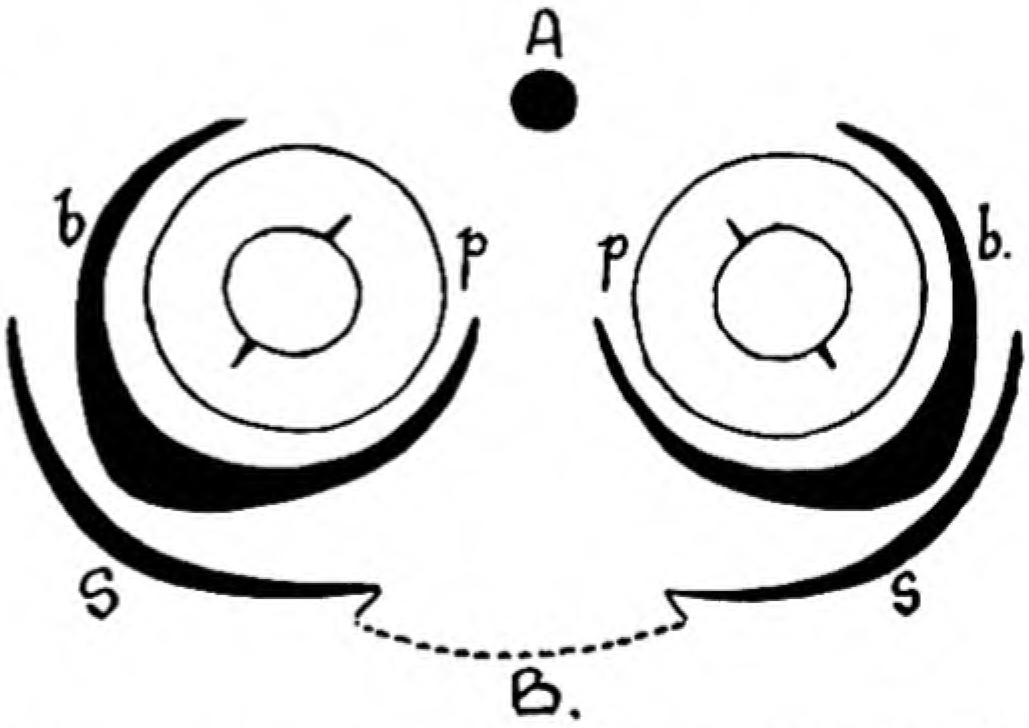


Fig. 221, c. Diagram illustrating Structure of Inflorescence of Hop.

A, Axis; B, bract; S, stipules of bract; b, bracteoles; p, perianth surrounding ovary of female flower.

11. Dispersal of Seeds and Fruits

It is manifestly of advantage to the species that the seeds should be carried some distance from the parent plant and be widely dispersed. It gives the young seedlings a better chance of survival, for they are saved, to a large extent, from competition with the parent plant and each other in the matter of food, light, etc. Arrangements for dispersal have an immense importance, also, in connexion with the study of the distribution of plants over the earth's surface.

The means of dispersal adopted by different plants vary widely, and are frequently such as to secure the almost ubiquitous distribution of some species. The four commonest agencies by which dispersal is secured are (1) **wind,** (2) **water,** (3) **animals,** (4) **explosive** or **ejection mechanisms** in the fruit itself.

12. Dispersal by Wind

Dispersal by wind is facilitated by many different arrangements and contrivances. It should be noticed that it is only in the case of *dehiscent* fruits that the mechanisms are borne by the seed; closed fruits and the segments (mericarps) of splitting fruits are themselves distributed, and possess contrivances aiding dispersal.

(*a*) The seeds of some plants (e.g. orchids) are so small and light that when they are set free from the fruits they are freely blown about by the wind.

(*b*) "*Censer mechanisms.*"—When the seeds are larger and heavier the fruit frequently opens in such a way that the seeds can only escape a few at a time, and are jerked out when the plant sways in a high wind. This censer mechanism is seen in follicles (e.g. *Aconitum*), in many capsules which dehisce by pores (*Papaver* and *Campanula*), or by teeth (Caryophyllaceae, *Androsace*, *Lysimachia*), and in some capsules with longitudinal dehiscence (lily and iris); it is also seen in the fruiting heads of some Compositae where the achenes have no pappus, e.g. *Helianthus*.

(*c*) As an aid to wind-dispersal, seeds are frequently flattened (e.g. some Cruciferae), as also are the fruit-segments of some Umbelliferae, and the achenes of Ranunculaceae, Rosaceae and some Compositae.

(*d*) "*Parachute mechanisms.*"—Special structures of the nature of wing-like or hairy outgrowths are frequently present which enable the seeds or fruits to be more readily carried by wind. The **plumed seeds** of *Cochlospermum*, Apocynaceae, Asclepiadaceae, and *Gossypium* have hairy outgrowths. **Winged seeds** are found in *Gordonia*, *Pinus*, Bignoniaceae. Good examples of **winged fruits** are seen in the samaras of *Ulmus*, Sapindaceae, and Apocynaceae. In *Tilia* (Fig. 267), the stalk bearing the cluster of nuts hangs down and the large bract attached to it gives buoyancy. In *Rumex* the fruit is covered by the calyx which bears three wings (Fig. 249). Other Polygonaceae and Chenopodiaceae show similar adaptation of the perianth. In *Carpinus* the three-lobed wing is formed from the persistent bract and bracteoles (Fig. 243). In *Shorea* the three outer sepals form a wing. As examples of **plumed fruits** we have the achenes with persistent hairy styles of *Clematis* and *Naravelia*, and the pappus-crowned cypselas of many Compositae (Fig. 214, A). In *Rhus* the persistent panicle becomes plumose. It is interesting to notice the various ways in which these structures are developed.

Dispersal by wind involves a greater loss of seeds than dispersal by animals, for the latter usually frequent fertile localities where the seeds have a chance of germinating, whereas wind-dispersed seeds may fall upon sterile or unsuitable localities, or may be carried out to sea. Wind-dispersed seeds are usually produced in relatively greater abundance than those dispersed by animals.

13. Dispersal by Water

Special adaptations ensuring dispersal by water occur chiefly in plants growing in or near water. In some cases the fruits are fibrous and contain air and can float, e.g. *Cocos*, *Barringtonia*, *Cerbera*, etc. In certain mangrove plants the seedlings can float in water until they become stranded in the mud. In *Nymphaea* and *Nelumbium*, the seeds are able to float as they are provided with a spongy covering (aril) containing air.

14. Dispersal by Animals

Seeds and fruits may be dispersed by animals, either by adhering to them or by being eaten by them.

In the former case certain structures, of the nature of hooked spines, are developed by which the fruits or seeds become attached to the fur or wool of passing animals. These adhesive structures are usually outgrowths of the fruit and not of the seed. Examples are found in *Urena* and *Cynoglossum*, *Chrysopogon aciculatus* has barbed awns. In *Geum* (Fig. 255, C) the persistent styles are hooked. In *Agrimonia* the hooks are developed on the receptacle of the flower which encloses two achenes. The flower-heads of *Dipsacus* have hooked involucral and floral bracts so that a passing animal may catch the plant and drag it forward, the rebound causing the fruits to be jerked out. In *Arctium* the involucral bracts of the capitula become hooked after the florets wither and whole burs (fruit-heads) may thus catch on to animals and be carried off. In *Bidens pilosa* each cypsela has a pappus of two to six stiff bristles covered with small downward-pointing prickles.

Succulent fruits, e.g. drupes, berries, pomes, etc., are eaten by animals. The succulent character encourages this mode of dispersal. The seeds are protected either by a resistant testa (berries) or a pericarp (e.g. *Fragaria*, *Rosa*), or by the seed being enclosed in a strong endocarp (drupes). In many cases the seed can pass through the animal's body without being injured, and if deposited in suitable soil may succeed in germinating. Very often, however, the hard part of the fruit is never swallowed, but allowed to fall to the ground after the soft part has been pecked, for the animals concerned in this mode of dispersal are usually birds whose gizzards may crush small seeds and destroy them.

Here again it is interesting to notice from what various parts the succulent mass may be developed —e.g. ovary-wall in drupes, receptacle in pomes, strawberry, and wild rose, perianth in mulberry, the aril in some seeds (e.g. mangosteen).

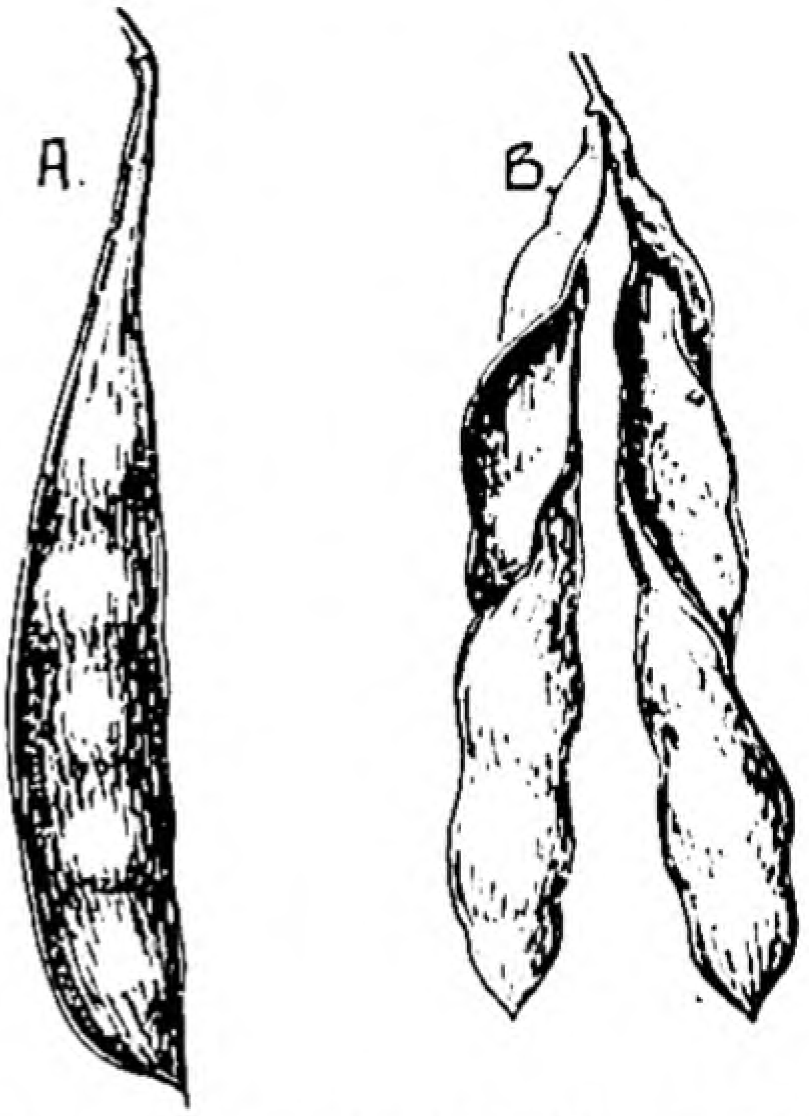


Fig. 222, A. DEHISCENCE OF POD OF LABURNUM.

15. Explosive Fruits

Some fruits show active movements by which the seeds are scattered or flung out suddenly. These movements often depend upon extreme turgidity in some part of the fruit, e.g. in squirting cucumber and balsams, or of the seed itself. In some species of *Impatiens* the fleshy capsules have swollen and stretched walls, so that a slight disturbance causes the capsule to burst and the seeds are thrown a few feet away.

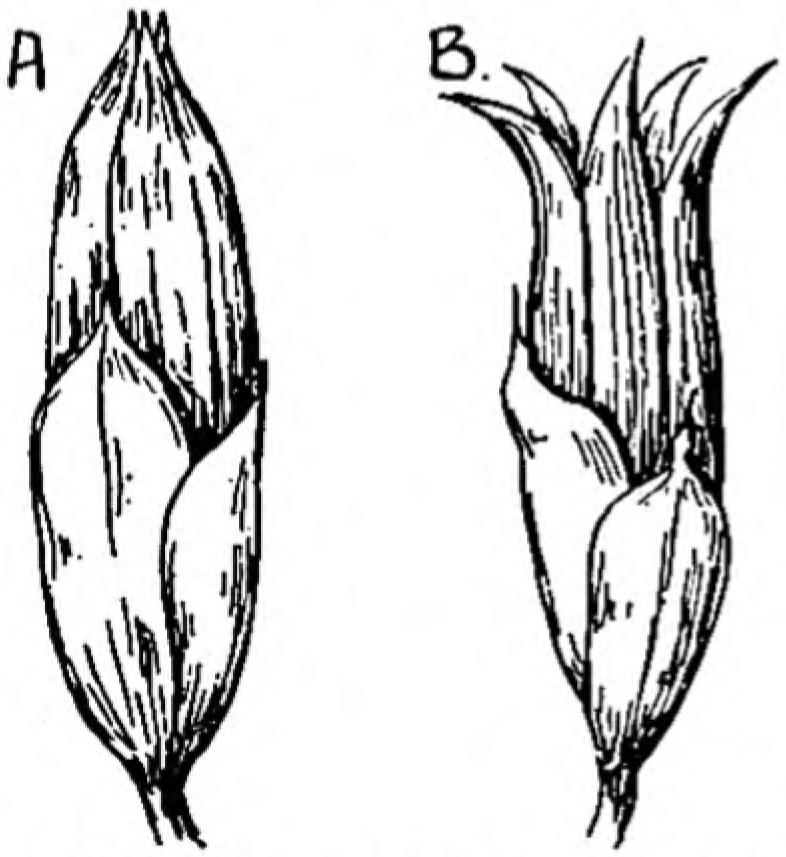


Fig. 222, B. DEHISCENCE OF CAPSULE OF *Dianthus*.

In some dry fruits the ejecting mechanism depends upon tensions set up by the drying of the fruit-wall. In *Viola* the capsule splits longitudinally into three concave valves, which by their contraction flick out the smooth, slippery seeds to a considerable distance. In *Geranium* the styles, by which the carpels remain attached to the carpophore (Fig. 219, C), suddenly curl upwards and outwards so as to throw out the seeds. The ripe pods of *Abrus*, *Cytisus*, *Lupinus*, etc., suddenly burst open, the two valves becoming twisted and the seeds scattered (Fig. 222, A).

The seeds of *Oxalis* have a fleshy aril, which is very elastic. When the capsule opens the aril suddenly turns inside out and jerks the seed away.

16. Occasional Dispersal

Seeds and fruits may *chance* to be dispersed in other ways. Many, which are adapted to other modes of dispersal, float when they happen to fall into water, and may be carried a considerable distance in this way. Others are carried on floating timber and in the mud adhering to the feet of water birds. Various seeds and nuts carried away for food by herbivorous animals may not be used by them. Here also we must include the dispersal of seeds and fruits by the agency of man. These occasional means of dispersal are, of course, accidental and additional to any method suited to the mechanism of the particular seed or fruit.

17. Analysis of the Classification of Fruits

The classification of fruits adopted in this chapter is neither complete nor perfect. Other characters which may be taken into account are (*a*) whether derived from a superior or inferior ovary, (*b*) whether from an apocarpous or syncarpous ovary, and (*c*) whether derived from the ovary only (true fruits) or whether other parts of the flower, such as receptacle, perianth, bracts enter into the structure (false fruits). The use of such additional characters in classification necessitates the recognition of a much larger number of kinds of fruits, and hence of descriptive terms. Within the scope of this textbook it is impossible and unnecessary to describe all the different kinds of fruits to which names have been given. Relatively few students are concerned with this aspect of botany. Further information as to fruit structure may be obtained by reference to the families of flowering plants described in Chapter XIII.

An analysis of the classification given in this chapter is set out below:—

A. Simple Fruits (product of the gynaeceum of one flower)

A. DRY

I. ACHENIAL

a. achene,	$(\underline{G})$, dock, sorrel, and some other Polygonaceae. $\underline{G}$, aggregate (etaerio), some Ranunculaceae and Rosaceae.
b. cypsela,	$(\overline{G})$, Compositae.
c. caryopsis,	$(\underline{G})$, Gramineae.
d. samara,	$(\underline{G})$, *Fraxinus*, *Ulmus*, Malpighiaceae, *Ailanthus*.
e. nut,	$(\overline{G})$, *Corylus*, *Quercus*, *Fagus*, *Castanea*, *Thesium*, *Elaeagnus*.

II. Capsular

a. follicle, $\underline{G}$, aggregate, some Ranunculaceae and Rosaceae, *Magnolia, Asclepias, Kalanchoë, Strophanthus.*

b. legume, $\underline{G}$, Leguminosae (Papilionatae).

c. siliqua, $(\underline{G})$, some Cruciferae.

d. silicula, $(\underline{G})$ some Cruciferae.

e. capsule, dehiscence porous, $(\underline{G})$, *Papaver, Antirrhinum.*
$(\overline{G})$, *Campanula, Ludwigia.*

dehiscence by teeth, $(\underline{G})$, Caryophyllaceae, *Reseda.*
$(\overline{G})$, *Lobelia.*

dehiscence by lid (pyxidium), $(\underline{G})$, *Anagallis, Hyoscyamus, Plantago.*

dehiscence valvular loculicidal, $(\underline{G})$, *Scilla* (Liliaceae), *Viola*, Acanthaceae.
$(\overline{G})$, Iridaceae, *Epilobium.*

dehiscence valvular septicidal, $(\underline{G})$, *Digitalis, Gentiana, Colchicum, Rhododendron, Linum.*
$(\overline{G})$, *Aristolochia.*

dehiscence valvular septifragal, $(\underline{G})$, *Datura.*

III. Schizocarpic

a. lomentum (lomentaceous legume), $\underline{G}$, *Hedysarum, Arachis, Tamarindus, Entada, Mimosa.*

lomentum (lomentaceous siliqua), $(\underline{G})$, *Raphanus.*

b. cremocarp, $(\overline{G})$, Umbelliferae.

c. carcerulus, $(\underline{G})$, Labiatae, Boraginaceae, Malvaceae.

d. regma, $(\underline{G})$, Geraniaceae, *Ricinus, Euphorbia.*

e. double samara, $(\underline{G})$, *Acer*, Malpighiaceae.

B. SUCCULENT

I. Drupaceous

drupe *a.* $\underline{G}1$, *Prunus* species, mango.
b. $(\underline{G})$, *Ilex, Cocos, Olea.*
c. $(\overline{G})$, *Cornus, Sambucus, Juglans.*
d. $\underline{G}$, aggregate, apocarpous: *Rubus* species.

II. Baccate

Berry *a.* $(\underline{G})$, *Vitis, Citrus, Phoenix, Lycopersicum.*
b. $(\overline{G})$, *Ribes*, Cucurbitaceae, *Musa.*

III. Pome

$(\overline{G})$, *Pyrus* species.

B. Composite Fruits (product of an inflorescence)

A. DRY

Strobilus, *Humulus.*

B. SUCCULENT

a. syconus, *Ficus*
b. sorosis, *Morus, Ananas, Artocarpus.*

CHAPTER XIII

CLASSIFICATION

1. Historical

The classification of plants was not seriously attempted until about the sixteenth century. Up to this period botanical knowledge had scarcely advanced since the time of the classical writers such as Theophrastus (372–287 B.C.) and Dioscorides (1st century A.D.). Moreover, it had become involved in a mass of superstition. The invention of printing made possible the publication of Herbals. At first these merely reproduced the inadequate descriptions of plants of the early writers, and the accumulated folk-lore associated with them. But the Revival of Learning stimulated thought and the spirit of enquiry. Men began to disentangle fact from fiction. Plants were re-examined, and careful descriptions and drawings were published. These were intended to ensure the correct identification of those plants to which were attributed certain medicinal properties. Further search and travel greatly increased the number of known plants and necessitated some sort of classification. Vegetative characters provided the basis for the earliest systems. This led, however, to incongruous results. For instance, all plants with grass-like leaves were placed in one group, those with bulbous swellings in another, and so on. Linnaeus (1735) used the characters of the sexual organs, and established twenty-four classes of plants. The twenty-fourth, the Cryptogamia, contained those plants whose sexual processes were not apparent to the investigators at that time. This system was convenient to use, and on this account was universally welcomed, but like all the rest, was essentially artificial.

A natural system of classification should be based on actual relationships. The doctrine of descent (Charles Darwin, 1859) provided a working hypothesis, and special morphology supplied the data by which affinities were suggested and conceptions of the phylogeny of plants built up. Studies in Fossil Botany, particularly during the last century, have added to our knowledge of the past history of plants. But even with all this accumulated knowledge of extinct and living plants, it is still not possible to trace an uninterrupted phylogenetic succession. It *is* possible to compare plants by taking into account all the morphological facts known about them. Those organisms agreeing in the largest number of characters are usually regarded as the most nearly related. But different systematists have evaluated the facts in different ways, so that several schemes of classification have been put forward, and later, perhaps, modified to fit new facts.

The Spermatophyta in the Herbaria at Kew and the British Museum (Natural History) are arranged according to the system of Bentham and Hooker (Genera Plantarum, 1862–1883). Another system which has been widely adopted is that of Engler and Prantl (Die Naturlichen Pflanzenfamilien, and Engler and Gilg, Syllabus der Pflanzenfamilien, 1936). A standard British work of reference based on this system is that of Rendle (The Classification of Flowering Plants, Vol. I, 1904, Vol. II, 1925). A more recent work embodying new ideas is that of Hutchinson (The Families of Flowering Plants, I, 1923; II, 1934).

2. Nomenclature

In addition to the Sexual System of classification we also owe to Linnaeus the general application of the binomial system of nomenclature. As the term implies, two names are used to designate a plant. The first is the generic and the second the specific name. We can illustrate it by reference to common plants.

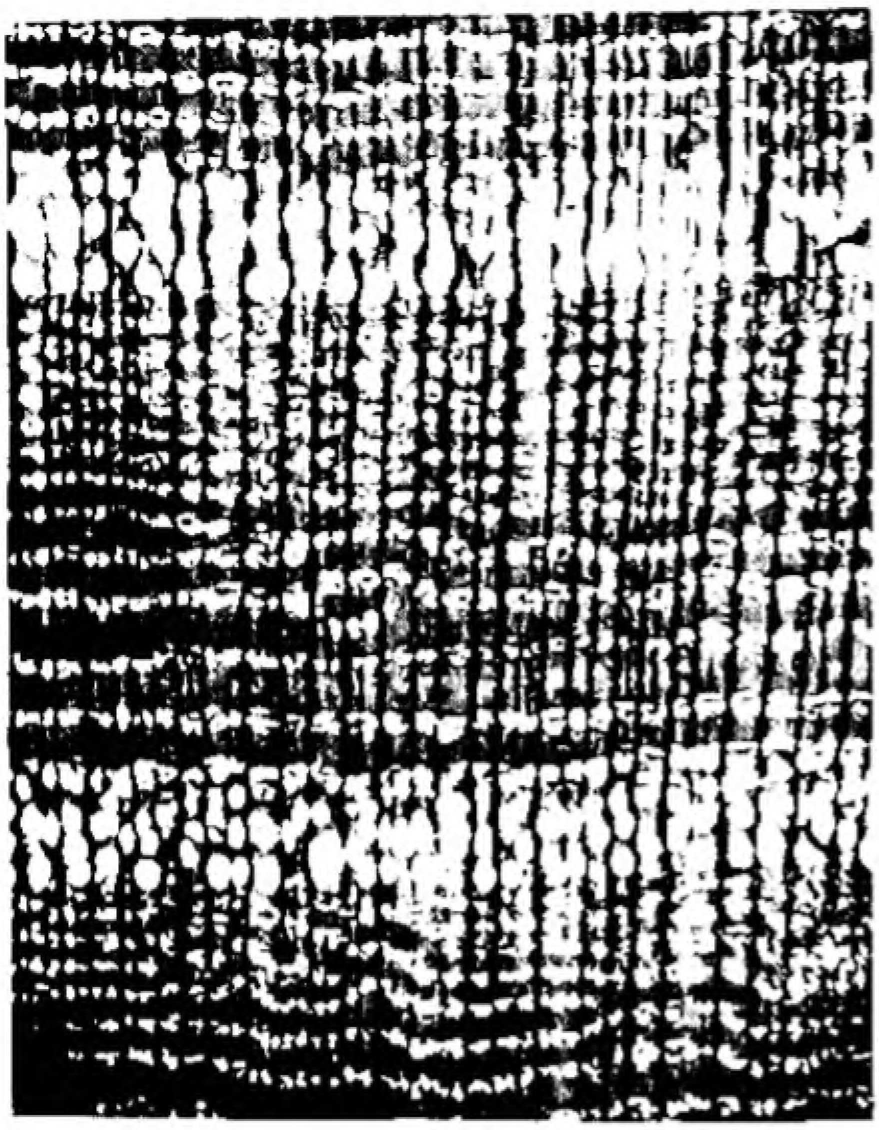
It is not difficult to recognise *Hibiscus* by its flower. But if *Hibiscus* plants are collected from different countries, localities or habitats, and compared, it will be found possible to arrange the individual plants in groups, the members of each group having similar features, but one group differing from another in one or more obvious characters. In the districts where they grow these plants may be known and distinguished by popular names, but such names may vary from district to district even in the same country. In India certain types of *Hibiscus*, for instance, have vernacular names such as Nir paratthi, Kandagang, Kondapatli, Okra, Bendekai, etc. It is important that each plant should have a name by which it may be known universally. Hence the value of the binomial system.

The **genus** *Hibiscus*, as we have seen, includes a number of different *kinds* or **species** named, it may be, according to shape of leaf, e.g. *Hibiscus vitifolius*, or to habit, e.g. *Hibiscus tiliaceus*, or to edible properties, e.g. *Hibiscus esculentus*, or after some person, e.g. *Hibiscus Solandra*, and so on.

Systematists are by no means agreed as to what constitutes a species. When plants are referred to by name, therefore, it is necessary to cite the authority for that name, and the recognised authority is the person who first publishes the name along with a suitable description of the plant. Sometimes drawings are also published, and a " type specimen " of the plant pressed and dried, and deposited in a herbarium for future reference. The authority for the genus *Hibiscus* is Linnaeus. He appears to have chosen a name used by Virgil for the marsh mallow (now known as *Althaea officinalis*, L.), and the first reference is in Genera Plantarum, Edition I, page 207, published in 1737. *Hibiscus lunariifolius*, Willd. refers to Willdenow, a German botanist who describes this plant in Species Plantarum, ed. III, p. 811, and *H. canescens* Heyne is No. 2689 in the Catalogue of the Wallich Herbarium. Sometimes different authors describe the same species under different names, or different species are recorded under the same name. Later investigation clarifies the position, but may leave a legacy of synonyms. Thus, *H. guineensis* G. Don is *H. lunariifolius* Willd., but *H. guineensis* DC. (A. de Candalle, Prodromus systematis naturalis regni vegetabilis) is *H. tiliaceus* L. (Species Plantarum).

Within some species a further sub-division into **varieties** may be possible. This variation may be the expression of the operation of one or more factors, e.g. the selective action of the environment. Generally speaking there is more intergrading between the varieties of a species than between the species of a genus. The earlier systematists, e.g. Linnaeus, Bentham and Hooker, favoured comprehensive species within which might occur a considerable amount of variation in vegetative morphological characters. Such variations may be, for a certain character, either continuous or discontinuous. In the former case, extreme forms are connected by a continuous series of intermediate forms, whereas in the latter, forms may fall into distinct groups, and it is in such cases that the systematist exercises his personal judgment in giving to such groups either varietal or specific rank. Sometimes differences between groups disappear when the plants are grown under the same conditions. It is important to remember that intermediate forms may be hybrids, that is, they may have arisen as the result of natural inter-crossing between groups. The more nearly related groups inter-cross readily and produce fertile offspring. This fact helps in determining relationships and in considering the limits of a species. Natural hybridisation between species of the same genus is not a common occurrence, and when it does occur, the offspring are usually sterile.

The species which compose a genus have usually a closely similar floral structure. They are differentiated by such characters as size of flower, colour of petals, form of sepals and petals, etc. The species may, however, differ very much in vegetative habit. Some species of ***Euphorbia***, for instance, which inhabit very dry places, so closely resemble species of Cactus that it is difficult to distinguish them when not in flower. Wide variation of vegetative habit is seen in other genera, e.g. *Crassula* and *Senecio*. Many vegetative characters have no value in a natural system of classification, as they are too variable. Floral characters are least subject to fluctuations in environmental conditions and are therefore more reliable for purposes of classification.



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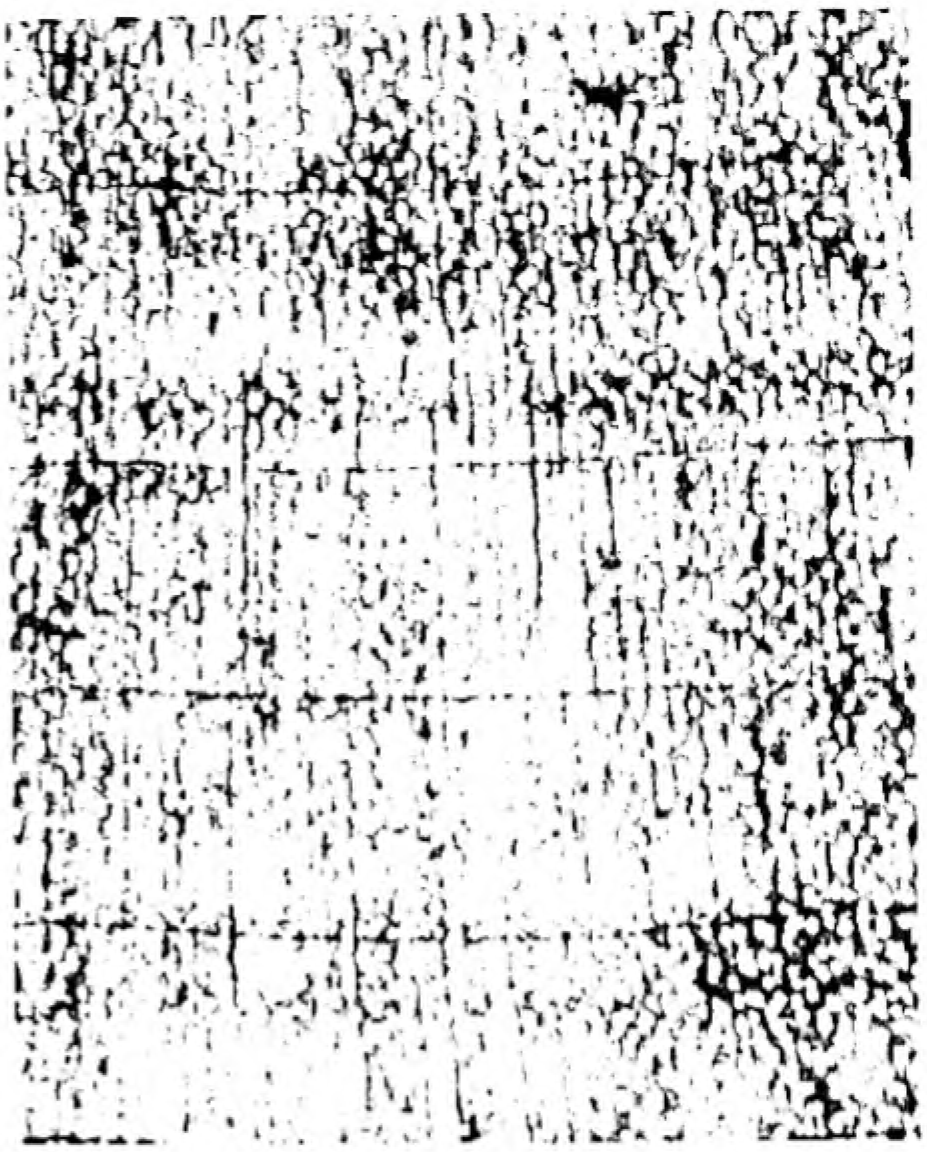

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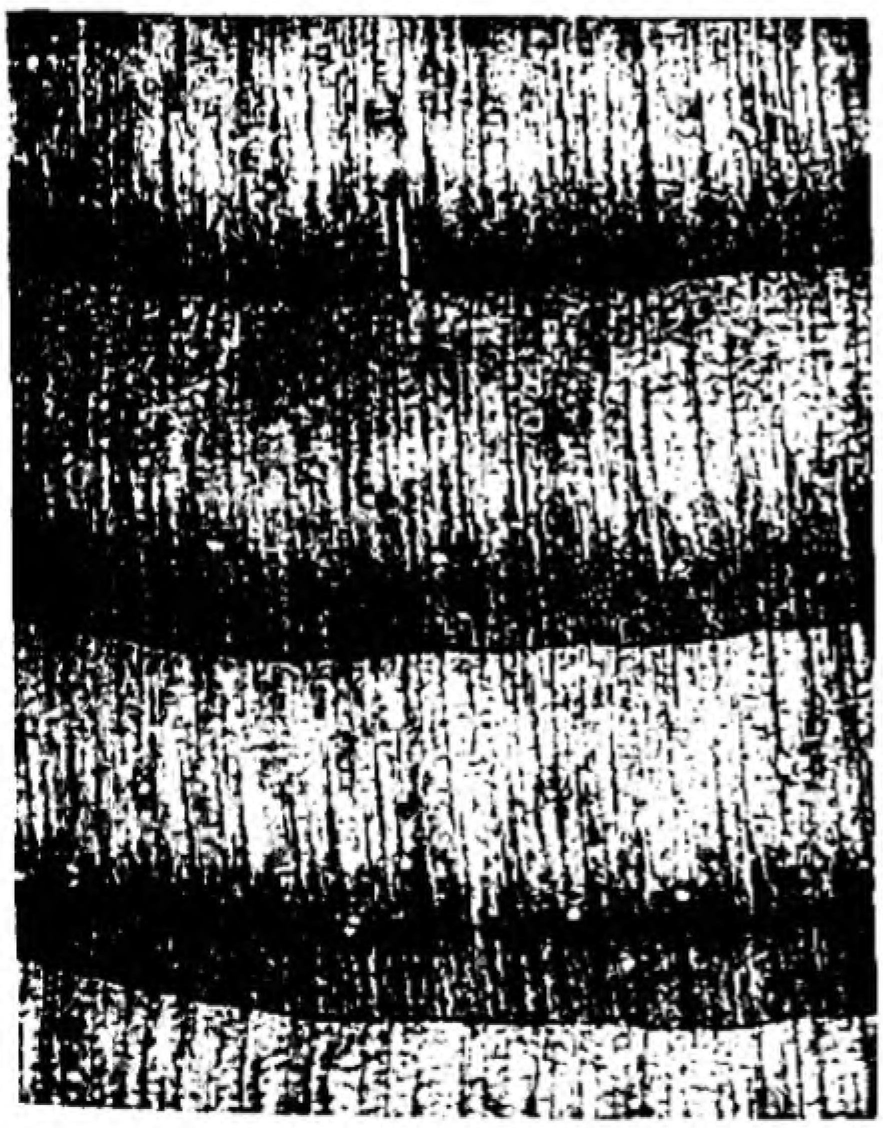

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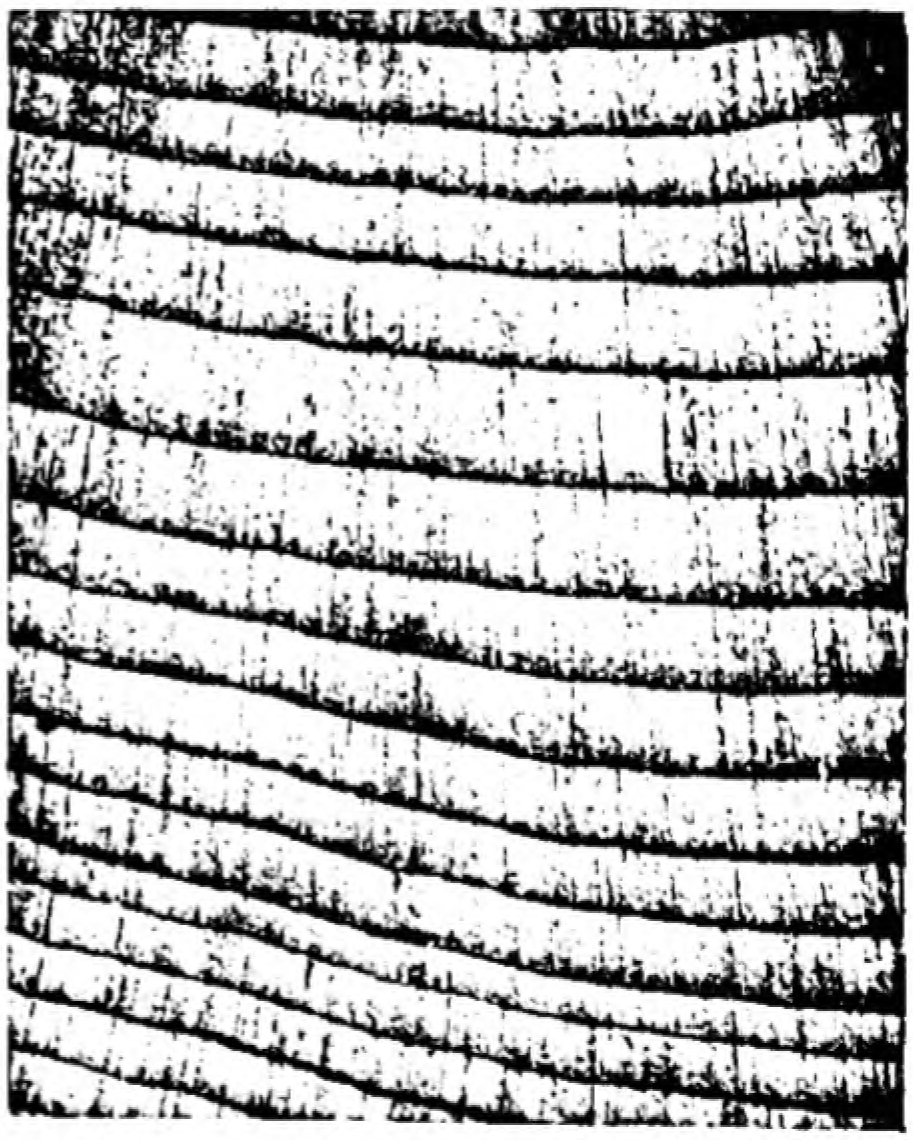

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PLATE V

1. Elm, T.S. Wood × 10. Ring Porous.

2. Birch, T.S. Wood × 10. Diffuse Porous.

3. Pine, T.S. Wood × 10. Tracheides and Resin Ducts.

4. Yew, T.S. Wood × 10. Tracheides, no Resin Ducts.

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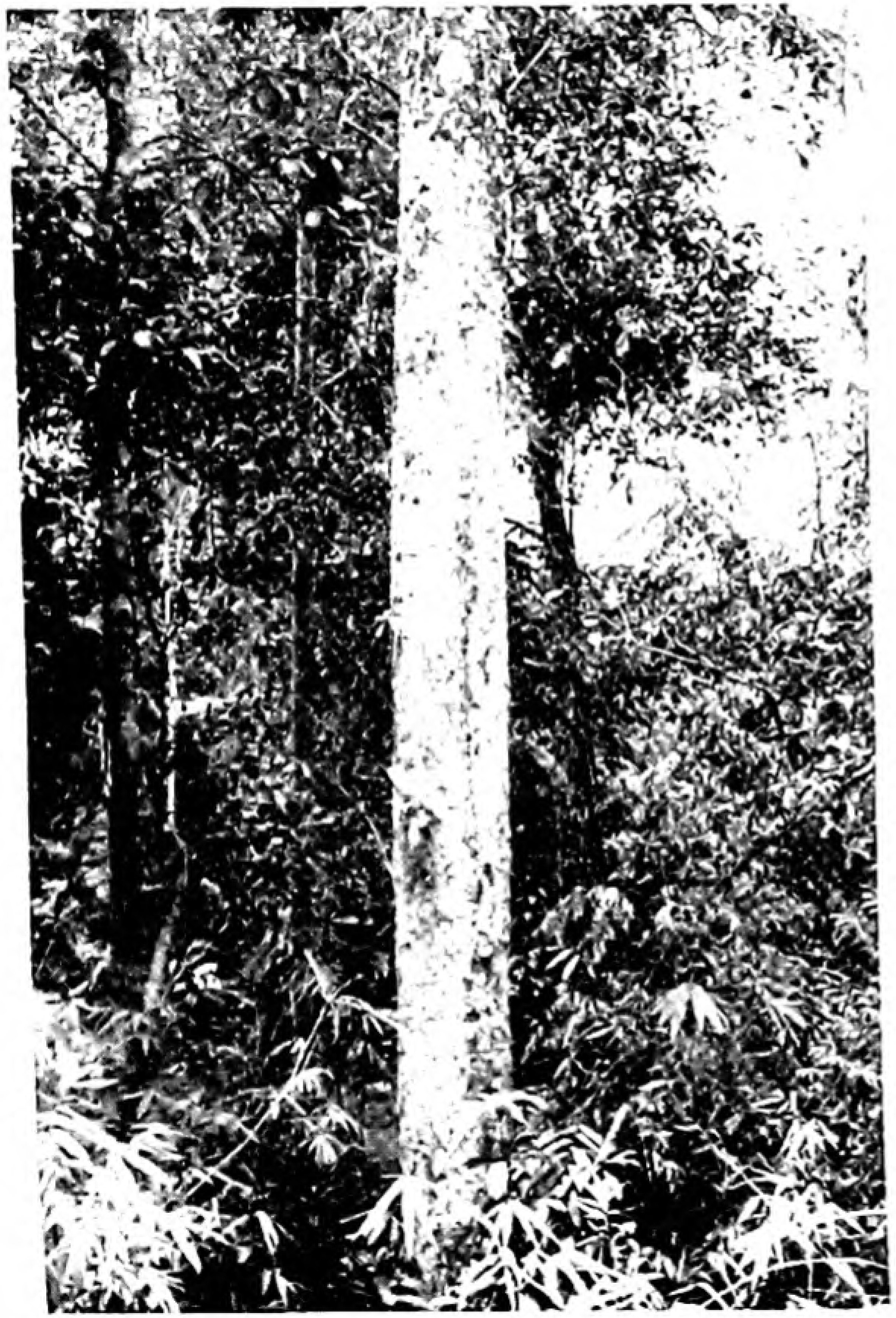

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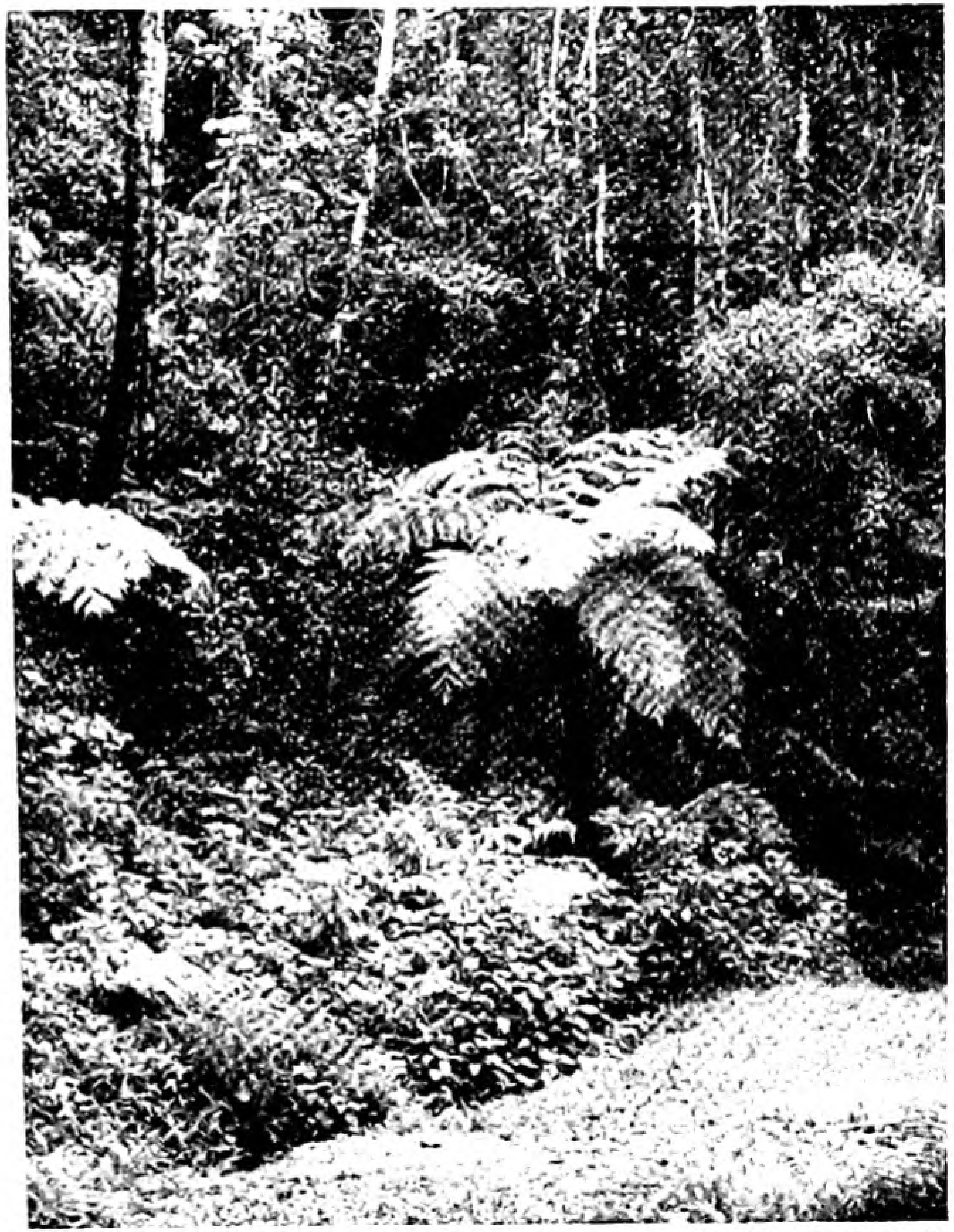

Photos N.G.B.

PLATE VI

1. Rain-Forest. The large straight tree is *Dipterocarpus zeylanicus*.

2. Hill-Forest in Ceylon. Altitude about 6,000 ft. In the foreground are tree-ferns (*Alsophila crinita*).

Closely related genera are grouped together into **Families** or **Natural Orders** usually denoted by names ending in -aceae, e.g. Ranunculaceae, but with some exceptions (e.g. Leguminosae, Compositae, Labiatae, etc.). The flowers of these genera show a general structural resemblance, although differing in details. Also characters of fruit and seed may be taken into account. The genera of a Family tend to agree in fewer characters than do the species of a genus, and their common ancestry would be much further back in time.

Families are arranged in orders or cohorts, and these in series, classes and groups. The whole conception is that of a genealogical tree, of which we only have left the tips of the branches, represented by existing species. The systematist studies these species, and from their characters, and those of fossil plants which have been sufficiently well-preserved in the various geological strata, he arranges them according to his conception of their mutual relationships.

3. Classification of Angiosperms

It is impossible, within the scope of this textbook to give a complete classification of the Angiosperms, or even to describe a sufficient number of Families to give a phylogenetic picture. We can only present a skeleton classification and deal with the more common Families represented in India.

SPERMATOPHYTA

Sub-division I. **Gymnosperms**: ovules naked on megasporophylls, no stigma, megaspores filled with prothallus tissue which becomes endosperm after fertilisation.

Sub-division II. **Angiosperms**: ovules enclosed in an ovary formed by one or more megasporophylls (carpels), stigma present, endosperm tissue, when present, formed after fertilisation. Angiosperms are divided into two classes:—

Class I. MONOCOTYLEDONS: embryo with one cotyledon, stem with vascular bundles usually closed and scattered, leaf-venation usually parallel, flowers usually with a 3-merous perianth.

A. Floral parts variable in number, e.g. Orders, Glumiflorae, Principes, Spathiflorae.

B. Floral parts typically in five 3-merous whorls, e.g. Orders, Farinosae, Liliiflorae, Scitamineae, Microspermae.

Class II. DICOTYLEDONS: embryo with two cotyledons, stem with open vascular bundles usually in one ring, leaf net-veined, flowers often with calyx and corolla, parts 2-, 4- or 5-merous. There are two sub-classes of Dicotyledons.

Sub-class 1. **Archichlamydeae**: perianth may be absent, single or double. Corolla, if present, polypetalous (rarely gamopetalous).

Orders.—Fagales, Urticales, Polygonales, Centrospermae, Ranales, Rhoeadales, Rosales, Geraniales, Sapindales, Malvales, Parietales, Opuntiales, Myrtiflorae, Umbelliflorae.

Sub-class 2. **Metachlamydeae** (Sympetalae): perianth in two whorls, corolla, with few exceptions, gamopetalous, stamens twice as many as the petals, or as many, or reduced to 4 or 2, epipetalous (exceptions, Ericaceae, Campanulaceae).

Orders.—Ericales, Primulales, Contortae, Tubiflorae, Rubiales, Cucurbitales, Campanulatae.

4. Families of Monocotyledons

A. ORDER GLUMIFLORAE.—Comprises the grasses and sedges, flowers usually with much reduced perianth, protected by membranous bracts (glumes). Ovary superior, unilocular, one ovule.

FAMILY **Gramineae.**—Flowers hermaphrodite, rarely unisexual, with reduced perianth of which there are usually only two members in the form of scales (lodicules) at the base of the ovary; rarely, however, a third is present in the posterior position (Bambusae, *Stipa*), or all three are absent (*Alopecurus*). Stamens usually 3, rarely 1, 2, 6-∞. Ovary with one ovule which is bent over so as to turn the micropyle towards the base of the funicle. Stigmas 2, 3 or 1. Fruit a caryopsis rich in endosperm, with the embryo occupying the micropylar end, and lateral. Only *Melocanna* is without endosperm. Rarely the fruit is a nut or berry. The embryo has a characteristic structure (Figs. 41 and 214).

This is one of the largest families of flowering plants, of world-wide distribution. Nearly all are herbaceous with hollow internodes and jointed nodes. *Zea mays* (maize) and a few others have solid internodes, and the bamboos often grow to a great height. The leaves are alternate, and are usually arranged in two opposite series or orthostichies (divergence ½). They have long sheaths which may be entire or split on the side opposite the lamina (Fig. 99, D). The lamina is linear to almost ovate, and usually bears a ligule at the base. Many grasses are annual; but the majority are perennial and either have rhizomes, runners, or suckers, or develop a tufted habit by copious branching at the base.

The **inflorescence** is more or less complex. The flowers are arranged in spikelets, but the spikelets are grouped together in various ways to form compound inflorescences. In the wheat (*Triticum*), perennial rye-grass (*Lolium perenne*) and *Tripogon* the spikelets are arranged on a main axis forming a compound spike.

In many other species the spikelets are borne on numerous branches given off from the main axis; in these forms the inflorescence is a panicle of spikelets which may be loose, e.g. the oat (*Avena sativa*), or contracted and cylindrical, owing to the shortness of the branches, e.g. *Setaria* and *Pennisetum*. In the ragi (*Eleusine*) and hariale (*Cynodon*) the inflorescence is digitate, *i.e.* composed of 2 or more branches from the top of the stem.

The spikelet (Fig. 223, A) consists of a slender axis bearing a number of scales in two rows. The two basal scales, one on each side, are barren, *i.e.* have no flowers; they are called the **glumes.** The other scales are bracts with flowers in their axils; they are called the *lemmas, lower* or *outer paleae* or *flowering glumes*. The lemma sometimes bears a long process called an awn.

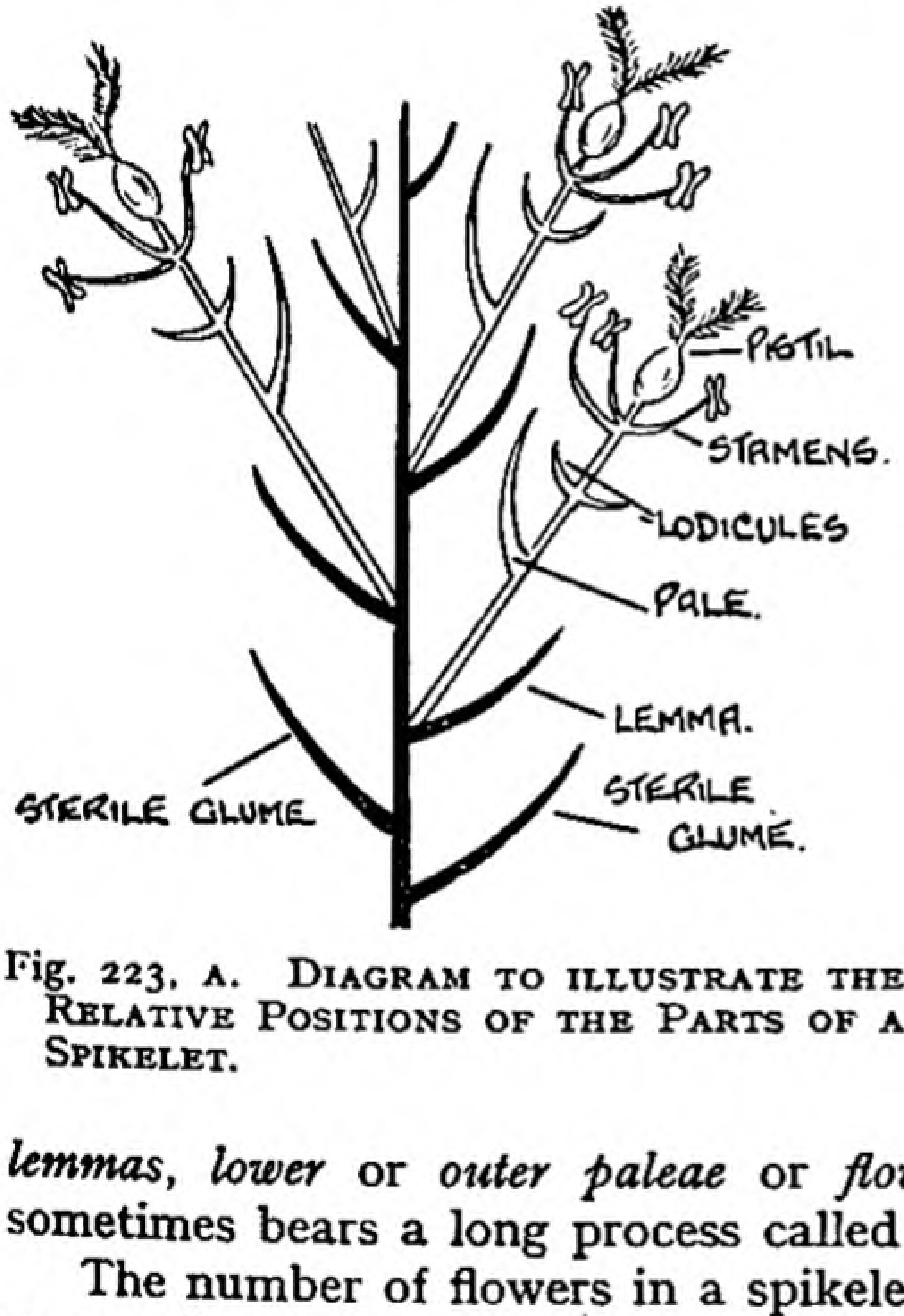

Fig. 223, A. Diagram to illustrate the Relative Positions of the Parts of a Spikelet.

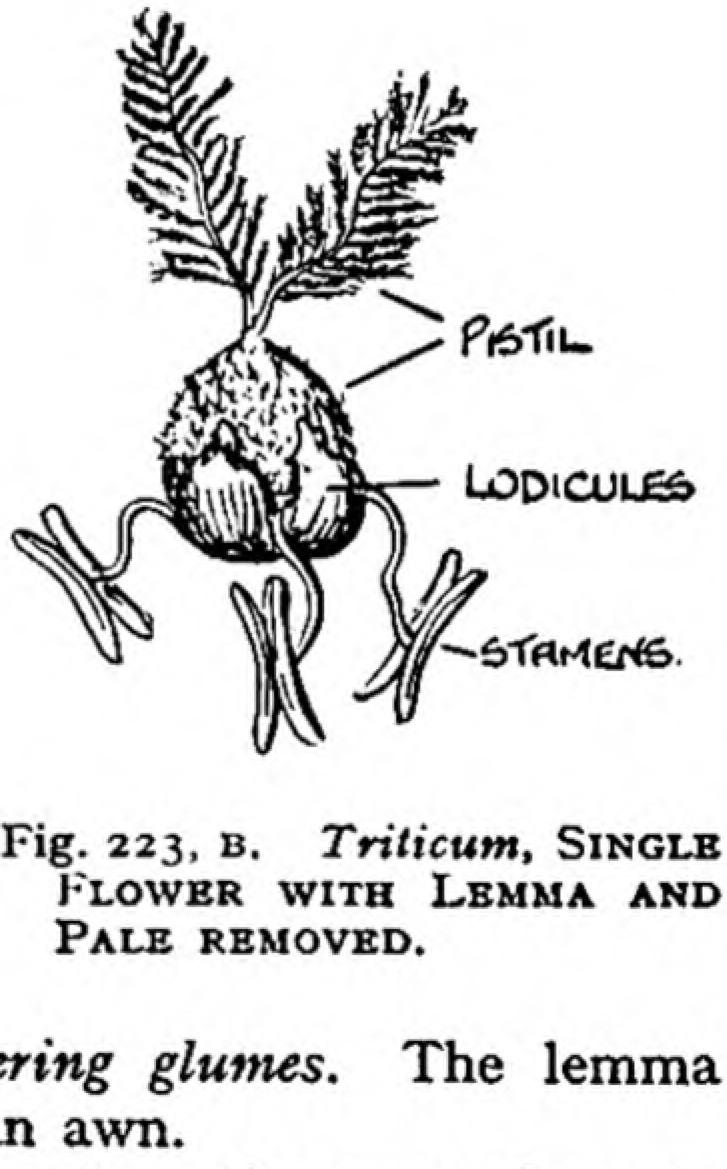

Fig. 223, B. *Triticum*, Single Flower with Lemma and Pale removed.

The number of flowers in a spikelet varies: there may be only one perfect flower; sometimes one or more of the flowers are rudimentary, e.g. the oat. The flowers are sometimes unisexual; in the maize male flowers are borne in a loose apical panicle, and female flowers on a stout lateral fleshy spike (spadix) sheathed in leaves.

The axis of the flower bears a scaly bracteole called the *palea* (or *pale*); it is opposite the lemma (*i.e.* posterior). The flower (Fig. 223, B) lies between the pale and lemma. It has usually three hypogynous **stamens**; sometimes six, or only two. The stamens have long slender filaments, and the anthers are versatile.

The **gynaeceum** is regarded as monocarpellary, and usually bears two feathery stigmas. The two stigmas are probably a development of the carpellary margins of the single carpel, not of the apex. The ovary is unilocular and superior, and contains one erect anatropous ovule. The **fruit** is a caryopsis (Figs. 41 and 214, C). The **seed** is endospermous.

At the base of the ovary on the anterior side (next the lemma) are two little scales called **lodicules.** These together may represent an upper bracteole. Some botanists consider that they represent two parts of a perianth of which the other parts are completely suppressed (Fig. 223, C).

Eleusine is a convenient type to study; also species of *Poa, Festuca, Bromus* and *Brachypodium* if available.

Pollination.—The flowers are protogynous and adapted for wind-pollination. At the time of flowering the lodicules swell and force the lemma and pale apart. The filaments of the stamens elongate and the anthers hang out. The microspores carried by air-currents are caught by the feathery stigmas. Most of the cultivated cereals, however, are commonly self-pollinated.

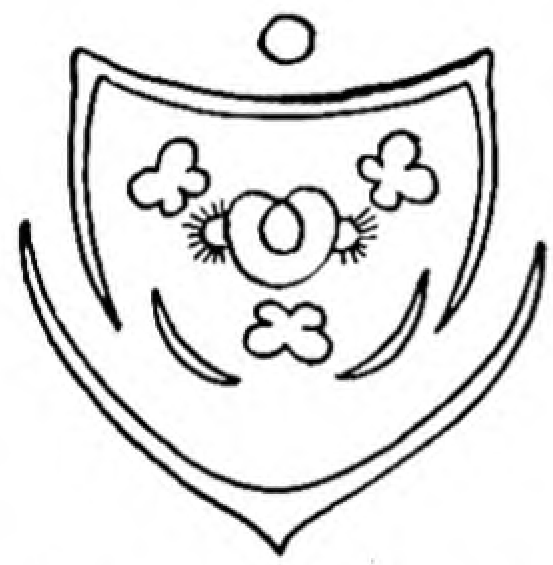

Fig. 223. C. *Triticum*—Floral Diagram.

Floral formula : K0 C0 A3 $\underline{G1}$.

The family is one of the most important, economically, in the world. The principal cereals are rice (*Oryza sativa*), wheat (*Triticum vulgare*), maize (*Zea Mays*), Italian millet (*Setaria italica*), Guinea corn, jowar or great millet (*Andropogon Sorghum*), bulrush millet, bajri or kumbu (*Pennisetum typhoides*), ragi or kurakhan (*Eleusine coracana*) and kikiyu grass (*Pennisetum villosum*).

Another important group of grasses includes the oil-yielding species. *Cymbopogon Nardus* is cultivated for its aromatic oil, citronella; *C. citratus* for lemon-grass oil; *C. flexuosus* for Malabar lemon-grass oil. *C. Martini*, geranium grass, is the source of rusa oil. *Andropogon squarrosus* (= *Vetiveria zizanoides*) yields the oil-bearing vetiver root.

Saccharum officinale is the sugar cane.

Quite a number of species are useful for fodder for cattle. Others are used in paper making and supply fibre which is used for cordage and mats, or their shoots are used for thatch. The hollow stems of the larger species are used for pipes. The bamboos supply many native requirements. They are used for buildings, scaffolding and for many domestic purposes; the split stems are woven into mats, baskets, fans, etc. *Spinifex littoreus* is a useful sand-binder on the sea shore. *Heteropogon contortus* (spear grass) has hygroscopic awns which cause the fruits to adhere to and penetrate the clothing of man and the wool of animals. The stony bracts of *Coix Lachryma* (Job's tears) are strung into necklaces. *Imperata cylindrica* is the cotton grass.

B. ORDER PRINCIPES.—Flowers usually cyclic, homoiochlamydeous, 3-merous, hypogynous, radially symmetrical, rarely feebly zygomorphic. Stamens usually 6, but also 3, 9 or ∞. Carpels 3, each with usually 1 basal ovule. Shoots monopodial without true secondary thickening. Leaves with palmate or pinnate venation. Inflorescence simple or compound.

FAMILY **Palmae.**—Flowers usually unisexual due to abortion (Fig. 224). Perianth sepaloid or semi-petaloid, rarely zygomorphic, the outer leaves often smaller than the inner. Stamens 6, rarely 3, or 9–∞, free or epiphyllous. Carpels 3, free, or when fused the ovary is 3- or 1-locular, usually, with 1 ovule per carpel. Fruit a berry or drupe. Seed rich in endosperm which is usually oily, often horny or ivory-like, with its whole surface firmly adherent to the stony endocarp in the drupes. Embryo small, lateral, the cotyledon becoming greatly enlarged in the seedling stage.

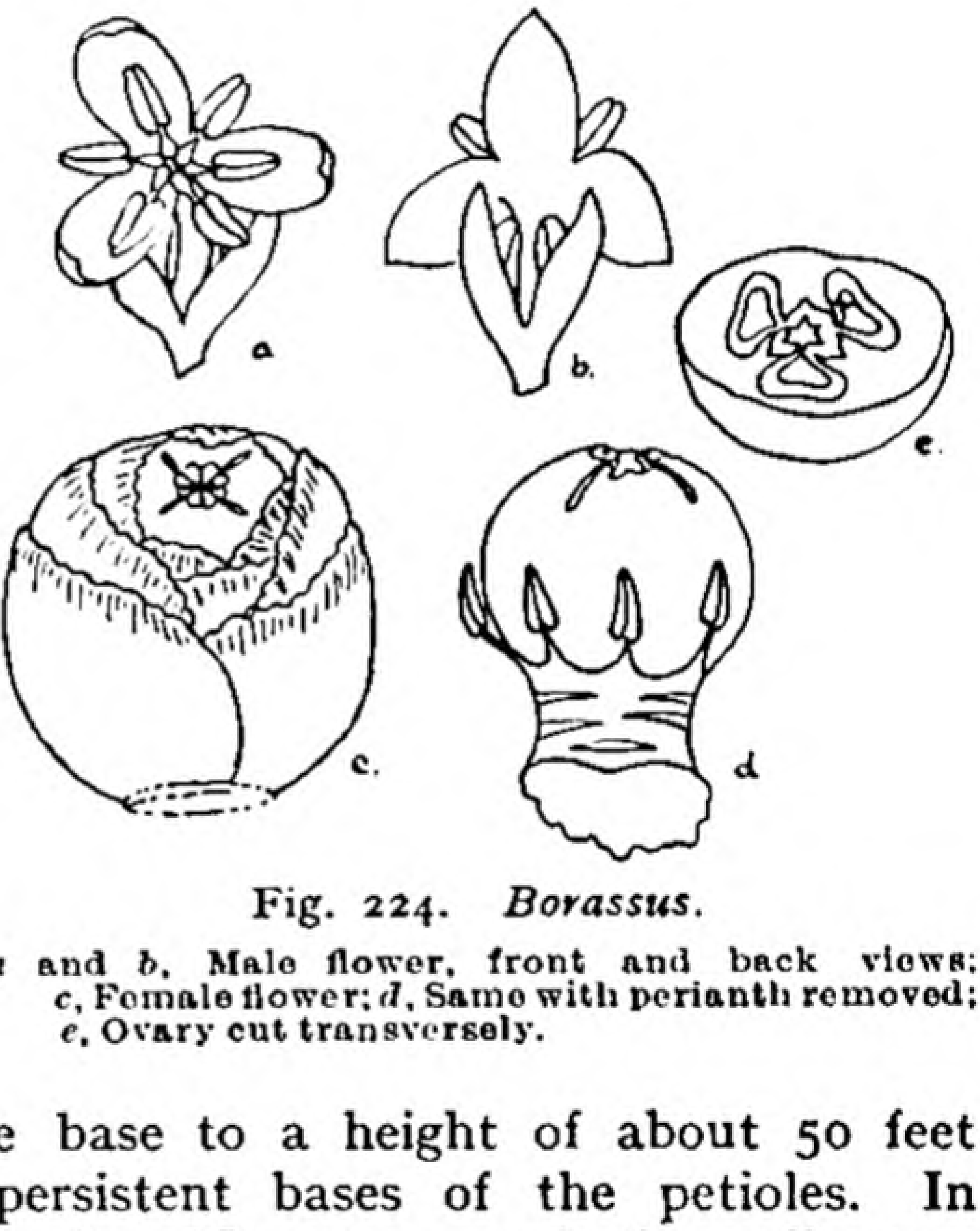

Fig. 224. *Borassus.*

a and *b*, Male flower, front and back views; *c*, Female flower; *d*, Same with perianth removed; *e*, Ovary cut transversely.

This is a large family of some 1200 species growing in tropical and sub-tropical countries.

The characteristic vegetative habit is a tall, straight stem bearing a crown of leaves. In the date palm (*Phoenix dactylifera*) the stem often rises in a curve from the base to a height of about 50 feet and is clothed with the persistent bases of the petioles. In the bastard sago or kitul palm (*Caryota urens*) the tall stem is smooth and shining, and is crowned with a few very large bipinnate leaves. In the talipot palm (*Corypha umbraculifera*), which may be up to 80 feet in height, the stem is stout and crowned with large, more or less circular leaves cut from the margin into numerous segments which are folded lengthwise. The stem of the palmyra palm (*Borassus flabellifer*) is swollen above the middle and then contracted towards the apex. The climbing habit is seen in the rattan palms (*Calamus* species), in whose leaves an entension of the rachis is provided with spiny claws which appear to be modified leaflets.

The leaves of palms are remarkable in their development. The massive lamina has either pinnate or palmate venation and is at first entire, but, as it grows it becomes split between the veins from the margin inward by the formation of an absciss tissue. In some palms this splitting may extend to the rachis, forming pinnae which are folded, reduplicate **Λ**, or induplicate **V** in transverse section. The leaf has a big sheathing base which is often very fibrous. The epidermis of the leaf is usually strongly cuticularised and glossy, but in some palms (e.g. *Copernicia*) the surface is covered with a layer of wax. The young leaves, as they emerge from the bud, do not open out until they have developed sufficient protection against excessive transpiration.

Most palms have a large and much branched inflorescence. The talipot palm produces a terminal inflorescence when about forty years old and dies after fruiting. Here the inflorescence may reach a height of 40 feet and contain several million flowers. The palm's extensive reserves of food are exhausted in the production of a large number of fruits. In other palms which flower repeatedly throughout their lives there is a great flow of food materials to the developing inflorescence. Drawers of toddy take advantage of this by tapping the peduncles, e.g. of *Caryota urens* and *Borassus flabellifer*.

Sometimes the inflorescences are in the axils of the current leaves, sometimes lower on the stem. In *Caryota urens* the inflorescences occur first from the upper leaf sheaths and then successively in descending order from the lower ones. The branching is racemose, and the inflorescence is enclosed in a spathe consisting of one or more leaves out of which it bursts when ripe. The individual flowers are sometimes free, but they are often sunk in the tissue of the axis, and the inflorescence is then termed a spadix (Fig. 198). Sometimes the palm is dioecious, sometimes monoecious, and in the latter case it often has the flowers in little dichasia of three, one female flower between two males, as, for instance, in *Caryota*.

The **flower** has usually a perianth of six segments in two whorls of three leaves, usually all free and alike in colour and texture. The stamens may be 3, 6 or numerous and the superior ovary of 3 or (3) carpels, in the latter case forming a 1- or 3-locular ovary with 3 (or only 1) anatropous ovules. Pollination may be by wind or insects.

The **fruit** is a berry or drupe of 1–3 loculi, with the endocarp united to the seed. The pericarp may be smooth, rough or (as in the sago palm) clothed in hard scales. The **seeds** are erect or laterally attached; the raphe usually sends out branches over the testa; the endosperm is large, and, as in date and ivory nut, consists of cells with thick cellulose walls and conspicuous pits (Fig. 16, A). In betel-nut the endosperm is ruminate, due to folds of the seed-coats into the endosperm tissue. These folds contain vascular bundles which branch from the raphe.

Several palms are cultivated in India and are important economically. The coconut palm (*Cocos nucifera*) yields food for man and cattle as well as valuable oil and fibre. It is grown chiefly near the sea. The flowers occur in spikes branching from a central axis and enclosed in a tough spathe over a metre long. Near the base of each lateral axis is a solitary female flower, and around the axis above it are numerous male flowers. The latter ultimately drop off, leaving the now naked axis as an appendage of the fruit.

Only one ovule of the 3-celled ovary develops into a seed. The fruit is therefore one-seeded. The pericarp differentiates into an epicarp forming a smooth and tough outer covering; a fibrous mesocarp consisting of numerous longitudinally arranged fibres, and an endocarp, or shell, which is hard and woody, and bears at one end three "eyes" corresponding to the three carpels. Through one of these "eyes" grows the embryo on germinating. Inside the shell is the seed, covered with a thin, light brown seed coat and enclosing an endosperm which forms the "meat" of the coconut. This is white and fleshy, and the cells contain numerous oil drops and aleurone grains. Within the endosperm is a cavity containing a watery fluid, the "milk," which makes a refreshing drink. The dried endosperm (*copra*) yields coconut oil and oil cake. Household articles are made from the shell, and the fibrous mesocarp gives coir fibre from which ropes, mats and brushes are made. The inflorescence is tapped when young for toddy, which when evaporated yields jaggery or sugar, and when fermented, arrack.

The leaves of the coconut palm may be woven into "cadjans" and employed for thatching or used for matting, basket-making, etc. The tissue of the stem has many uses. To cabinet makers it is known as porcupine wood; its peculiar appearance is due to the numerous scattered vascular bundles.

Equally important is the palmyra palm (*Borassus flabellifer*) which supplies many requirements of a large population. The outer tissue of the stem is hard and black, the inner tissue soft and light brown. It is used for building purposes, posts, fences, water-pipes and troughs. The leaves are employed for thatching, basket-work, hats, etc. The pulp of the fruit is eaten. The fibre of the leaf-bases is used for brushes. The young inflorescence is tapped for toddy. An ancient Tamil song in praise of this palm enumerates 801 uses to which it can be put. It occupies extensive areas in the drier portions of southern India.

Yet another important cultivated palm is the toddy or kitul palm, or bastard sago (*Caryota urens*). This is more specially used for toddy making, but its trunk, strong and durable, is used for building huts or for agricultural implements. The hollowed stems are used for water channels; the fibre of the petioles for fishing lines, and the pith of the stem for sago.

The areca or betel-nut palm (*Areca Catechu*) is largely cultivated in Bengal and other parts. Its nuts are sliced and chewed with the leaves of betel-pepper (*Piper Betle*), and the powdered nuts are also used as a vermifuge for dogs.

The talipot palm (*Corypha umbraculifera*) is a characteristic feature of the vegetation in the south. The leaves, cut into large pieces, are used as umbrellas, and cut into narrow strips form the pages of the old books upon which many sacred writings have been handed down. Writing upon them is done with a sharp metal stylus, then charcoal is rubbed in to make a permanent and indelible record. The pith of the stem is used for flour and the leaves for thatching. It is an ornamental tree.

The date palm (*Phoenix sylvestris*) occurs cultivated and wild, often in dense thickets. The fruit is edible, the stem is tapped for toddy and the leaves are plaited into mats. The leaves of *Nipa fruticans*, abundant in the Sundarbans and elsewhere on the coast, form the best cadjans. In the Malay peninsula, Ceylon, and the far south of India, the rattans (*Calamus* species) are the source of the rattan canes of commerce.

Other palms of economic importance are *Metroxylon Rumphii* of the Sunda Isles and the Moluccas, which yields the best sago; *Elaeis guineensis*, in tropical West Africa and the east coast of South America, which is the source of palm oil; and *Phytelephas* species, in tropical America, which yield vegetable ivory.

Sabal, or saw palmetto, comes from *Serenaea serrulata* (= *Sabal palmetto*), carnauba wax from *Copernicia cerifera* and *C. australis*, and dragon's blood from *Daemonorops* species.

C. ORDER SPATHIFLORAE.—Flowers cyclic, haplochlamydeous or homoiochlamydeous, or naked as the result of reduction, 3- or 2-merous, ☿ or ♂ ♀, often reduced to one stamen or one carpel, always arranged on a spike (or spadix) which is more or less enclosed in a spathe (Fig. 225, A).

FAMILY **Araceae.**—Flowers hermaphrodite or unisexual, 2- or 3-merous or reduced to one stamen or one carpel. Fruit usually a berry. Seed usually with two integuments of which the outer is fleshy. Commonly herbs with tuberous rhizomes, but some are shrubs or small trees, or lianes. Flowers usually monoecious, rarely dioecious, usually many, rarely only 2–3 per spadix or cluster. The leaves show great variety. About 1800 species, mostly tropical.

This family is well represented in the tropics. In India it includes the small floating *Pistia* (water-soldier or -lettuce), common in tanks and wells; marsh plants such as *Cryptocoryne*, *Lagenandra* and *Acorus* (sweet flag); and terrestrial plants, e.g. *Typhonium*, *Theriophonum*, *Ariopsis*, *Colocasia* and *Alocasia*. The two last named have tubers rich in starch and valuable as food. *Colocasia antiquorum* (taro) is cultivated and all parts of the plant are eaten. *Alocasia indica* is also cultivated for its edible stem and roots. *Remusatia vivipara* is an epiphyte which rarely flowers and propagates itself by bulbils. *Arisaema Leschenaultii* is known as the cobra flower on account of its dark-green spathe vertically striped with purple. The spathes of other species also resemble snakes. *Amorphophallus campanulatus* is widely cultivated for its edible tubers. *Lasia spinosa* has a thick rhizome and leaves spinous along the petioles and veins underneath. Climbing shrubby types may have two kinds of adventitious aerial roots; some which are negatively phototropic and attach the plant to its support, others which are positively geotropic, grow down to the soil and absorb nutrients. In *Pothos armatus* modified adventitious roots form spines.

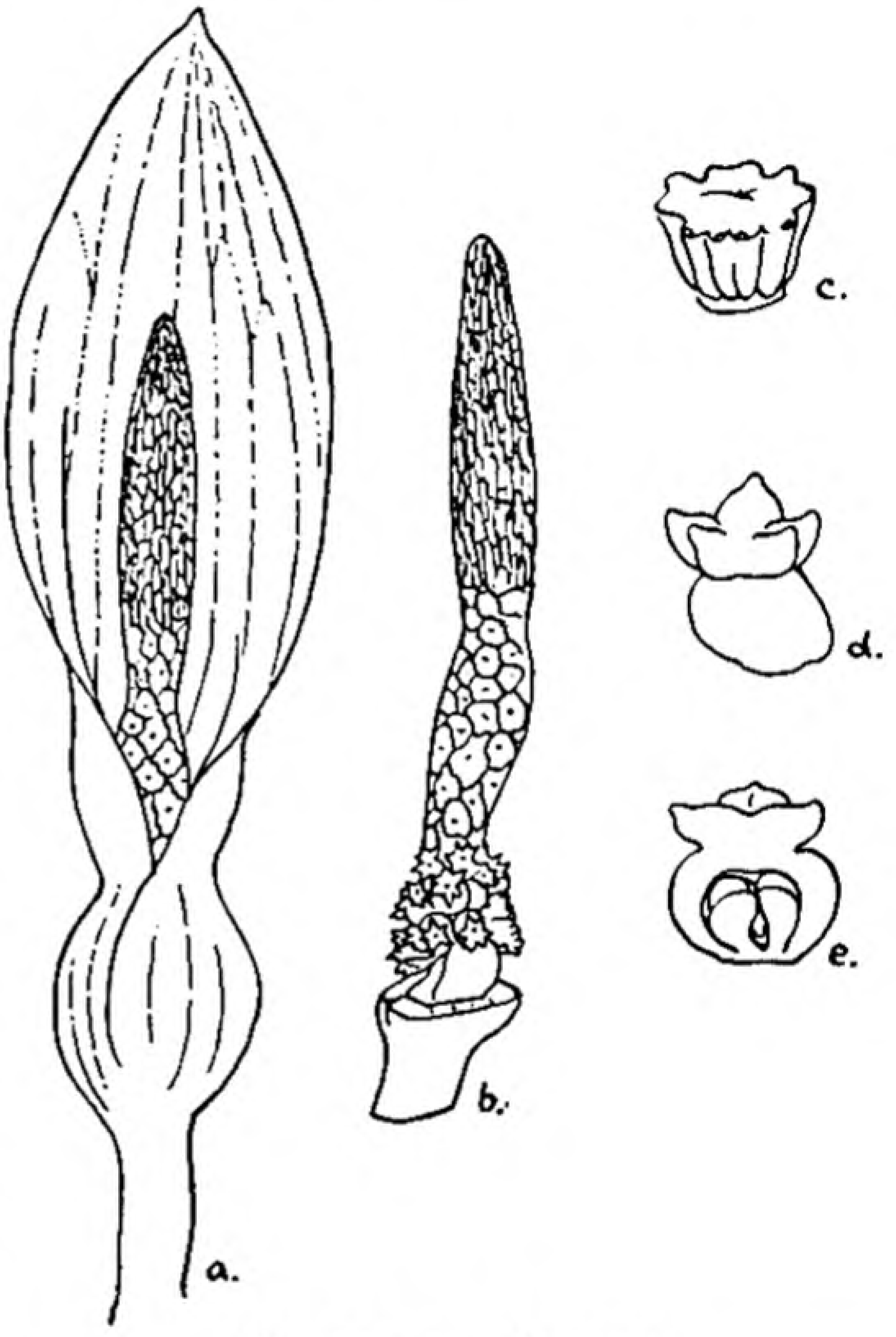

Fig. 225, A. *Alocasia*.

a, Spathe enclosing spadix; *b*, Spadix; *c*, Male flower *d*, Female flower; *e*, V.S. of female flower.

D. ORDER FARINOSAE.—Flowers cyclic, homoiochlamydeous or heterochlamydeous, 3- or 2-merous, typically $P3 + 3$ (rarely $K3\ C3$) $A3 + 3\ G(\underline{3})$. Stamens epiphyllous, all perfect or two or more reduced to staminodes, filaments often clothed with jointed hairs, anthers often dissimilar (Fig. 225, B). Ovary superior, 2–3 locular, ovules usually orthotropous, 1–several per loculus, axile placentation. Seeds with mealy endosperm.

FAMILY **Commelinaceae.**—Flowers heterochlamydeous, 3-merous, hermaphrodite, actino- or zygo-morphic. Carpels (3–2), stigma 1, ovary superior 3- or 2-locular each loculus with one orthotropous or anatropous ovule. Fruit usually a loculicidal capsule or indehiscent. Seeds endospermous, often with an arillus. Herbs with jointed stems and alternate sheathing leaves with narrow, often grass-like blades. Flowers in inflorescences of the cincinnus type, sometimes in panicles. Perianth usually blue, violet, yellow or white. Includes about 300 tropical and subtropical species, few temperate.

This is a small family, but spread over Old and New Worlds. In America it is represented by *Tradescantia*, *Dichorisandra* and *Rhoeo*; in tropical Africa by *Palisota* and in Asia by *Commelina*, *Aneilema* and others. Several are common weeds.

The family is mainly represented in India by a few common weeds belonging to the genera *Cyanotis*, *Aneilema* and *Commelina*. *Commelina benghalensis*, *C. obliqua* and *C. nudiflora* occur in most districts.

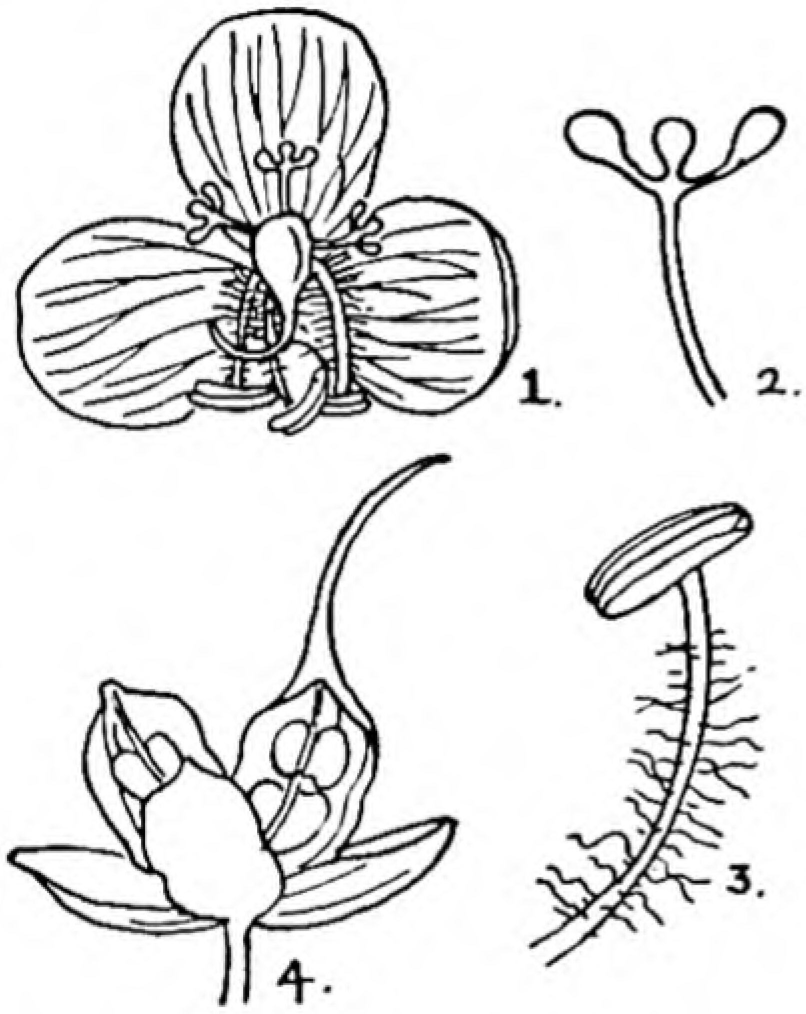

Fig. 225, B. *Aneilema*.
1. Flower; 2. Staminode; 3. Stamen; 4. Fruit, loculicidal dehiscence.

In *Tradescantia*, which is largely cultivated, all six stamens are functional. Their filaments bear long multicellular hairs in the cells of which protoplasmic streaming may be readily observed (see p. 216).

E. ORDER LILIIFLORAE.—Flowers cyclic, homoiochlamydeous or heterochlamydeous, trimerous (only rarely 2-, 4- or more), usually hermaphrodite, actinomorphic, rarely somewhat zygomorphic. Typical formula $P3 + 3\ \ A3 + 3\ \ G(\underline{3})$. Seeds with fleshy or horny (oil bearing) endosperm. Ovules usually anatropous.

1. Family **Liliaceae.**—Flowers usually homoiochlamydeous, hermaphrodite, actinomorphic, rarely zygomorphic. Perianth 3 + 3, petaloid or sepaloid, free or fused. A3 + 3, rarely one or more suppressed. Ovary superior, of 3 fused carpels, trilocular, axile placentation. Fruit various, usually a septi- or loculi-cidal capsule, or a berry. Endosperm fleshy or horny.

This is another large family of about 200 genera. The plants are mostly herbs perennating by means of rhizomes, e.g. Solomon's seal (Fig. 54) and *Disporum*; bulbs, e.g. lily, onion, squill, tulip (Fig. 58); or corms, e.g. the meadow saffron or autumn crocus (Fig. 57) and *Iphigenia*. A few are shrubs or trees, e.g. *Dracaena* and *Yucca*, often showing secondary growth (p. 110). Some show vegetative reproduction by means of bulbils, e.g. *Lilium bulbiferum*. Some are climbing plants, e.g. *Smilax* (p. 137) and *Gloriosa*. *Ruscus*, the butcher's broom, is a shrub with cladodes (Fig. 63), bearing unisexual flowers. *Asparagus* bears tufts of cladodes axillary to minute scales. Many species are xerophytic (e.g. *Aloe*).

The **inflorescence** may be racemose or cymose. The umbellate heads found in many, e.g. *Allium* and *Agapanthus*, are cymose. In the tulip there is a solitary terminal flower. The **flowers** (Figs. 195, C and 226) are actinomorphic, usually hermaphrodite, typically trimerous and hypogynous. rarely unisexual. The **perianth** consists of six parts in two whorls, and is usually gamophyllous, occasionally polyphyllous (e.g. tulip and *Gloriosa*). There are six **stamens** in two whorls, hypogynous or epiphyllous, with usually introrse anthers. The **pistil** is tricarpellary, syncarpous; the *ovary* trilocular, superior; the *ovules* indefinite, anatropous; the *placentation* axile. The **fruit** is usually a loculicidal (*Aloe*) or septicidal (*Gloriosa*) capsule, occasionally a berry (e.g. *Asparagus* and *Smilax*). The **seed** is endospermous.

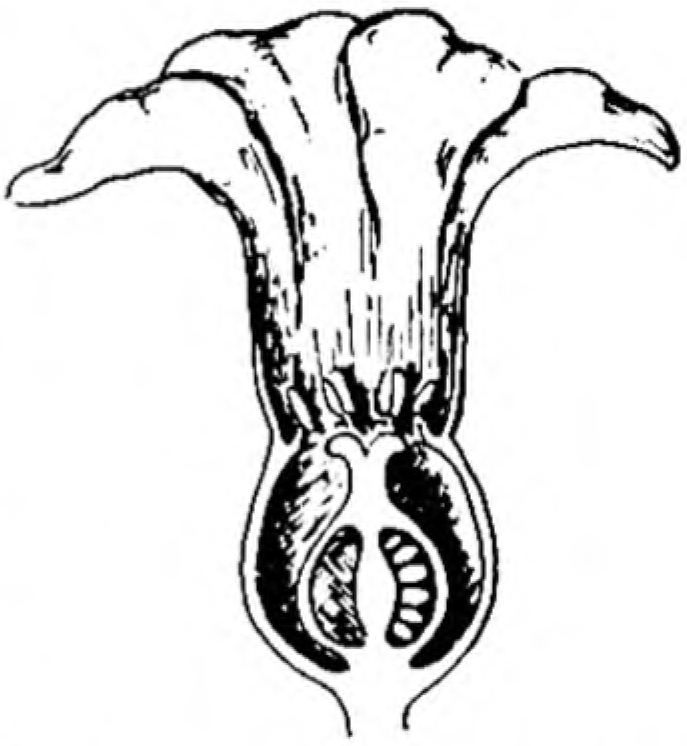

Fig. 226. Garden Hyacinth, half-flower.

In many cases the flowers are pendulous (the pollen being thus protected, and cross-pollination promoted), while the capsules are erect, and the seeds blown out gradually by the action of the wind (censer-mechanism).

Pollination.—Both self-pollination and cross-pollination occur, most of the flowers being adapted for long-tongued insects. In most cases nectar is produced by glandular tissue in the partitions between the chambers of the ovary (e.g. *Scilla non-scripta*, the bluebell). In *Lilium* it is secreted at the base of the perianth leaves; in the autumn crocus, on the outer side of the filaments of the stamens at the bases of their free parts. In tulip, garlic, and bog asphodel there is no nectar; the flowers are visited for pollen. In *Paris quadrifolia* the dusky colour and foetid smell of the flower attract carrion-loving flies.

In India this family is represented by a number of genera. *Asparagus racemosus* is common; the fruit is a berry. *Smilax* is a climbing plant with a pair of tendrils at the base of the reticulately-veined leaves (Fig. 100, G). The flowers are unisexual, the fruit a berry. The roots of some species yield Sarsaparilla. *Gloriosa superba*, the glory lily (Kulhári), is a climbing plant with a tuberous rhizome which is poisonous, and the leaf-tip is prolonged into a tendril; fruit a large septicidal capsule. *Sanseviera Roxburghiana*, the bowstring hemp, has a creeping rhizome bearing directly on it the long (about 60 cm.) leaves which yield a valuable fibre. *Aloe vera* has succulent leaves which yield Barbados aloes. *Dracaena terniflora* is a straggling shrub. Various species of *Lilium* grow in the more temperate mountain regions. *Asphodelus* species grow in the plains and lower hills. *A. tenuifolius* is a weed of fields and gardens in northern parts. *Urginea* has a bulb; the Mediterranean species, *U. maritima*, contains glycosides which make it a valuable rat poison. *Scilla indica* is the Indian squill. *Iphigenia* propagates by corms.

Allium Cepa, the onion or piáz, and *A. sativum*, the garlic or lassan, are cultivated for their edible bulbs. *Yucca gloriosa*, Adam's needle or egg-plant, is a valuable source of fibre used for carpets and mats.

2. FAMILY **Amaryllidaceae.**—Resembling the Liliaceae; stamens rarely in part staminodial, very rarely more than six. Anthers usually introrse. In many a corona is developed, regarded as the fused stipular appendages of the stamens. Ovary inferior, trilocular, axile placentae each bearing 2 rows of anatropous ovules. Fruit a capsule or berry, usually with few seeds. Typical floral formula $P3 + 3\ A3 + 3\ G(3)$.

The plants of this family mostly perennate by means of bulbs (e.g. *Crinum* species). A few have rhizomes, e.g. *Agave*. The leaves of *Curculigo orchioides* are often viviparous at the tips. Those of *Crinum* are fleshy. The species occur chiefly in hot, sunny, dry regions of the globe (S. Africa and S. America), their bulbs enabling them to tide over the dry, rainless season. They resemble Liliaceae in most of their characters, but are readily distinguished by the inferior ovary. There are few native Indian plants. They include *Hypoxis*, *Molineria*, *Curculigo*, *Crinum* and *Pancratium*. Amongst the cultivated and semi-wild forms are *Zephyranthes carinata*, the pink lily, and *Z. tubispatha; Agave americana* is the century plant; it is a xerophyte with rhizomes and massive rosettes of spiny leaves; after a vegetative period often of many years' duration it produces a huge inflorescence and then dies. This and other species of *Agave* have been planted for fibre. The leaves are thick and fleshy, and coated with wax. *A. sisalina* yields sisal hemp. *Furcraea gigantea* yields Mauritius hemp.

The **flowers** are produced on scapes, and are either solitary (snowdrop, daffodil) or two or more together in cymose inflorescences which are frequently umbellate (p. 257). A spathe is present (Fig. 227). The flowers are hermaphrodite, epigynous, usually regular and actinomorphic, occasionally zygomorphic.

The **perianth** is superior and petaloid. It consists of six segments in two series, and may be polyphyllous (snowdrop and snowflake) or gamophyllous (*Narcissus*). In *Narcissus* (Fig. 227) a cup-shaped or tubular corona is present (see p. 238). **Stamens** 6, either epiphyllous (*Narcissus*) or epigynous (*Galanthus*); anthers introrse or rarely extrorse. **Gynaeceum** tricarpellary, syncarpous; ovary trilocular, inferior; ovules ∞, anatropous; placentation axile; style single; stigma simple or trilobed. **Fruit** a loculicidal capsule, occasionally a berry (*Agave*). **Seed** endospermous.

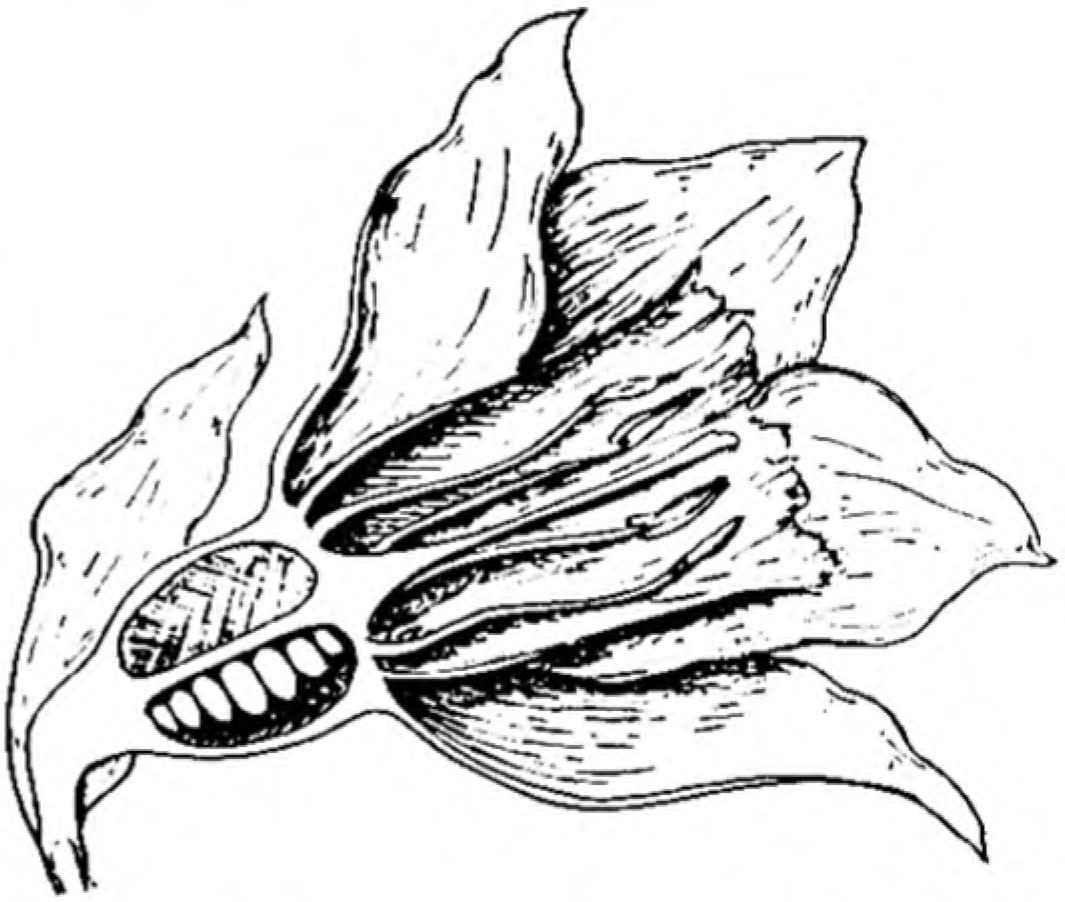

Fig. 227. *Narcissus*, HALF-FLOWER.

3. FAMILY **Iridaceae.**—Flowers (Fig. 228) homoiochlamydeous, or heterochlamydeous, trimerous, hermaphrodite, actinomorphic or zygomorphic. Stamens always only three, the outer whorl, with extrorse anthers. Stigmas three, frequently divided and petaloid. Ovary inferior, trilocular, rarely unilocular, with numerous anatropous ovules. Fruit a capsule with rounded or angular endospermous seeds.

The Iridaceae are largely represented in dry sunny countries (South Africa, Tropical America) by such plants as *Crocus*, *Iris*, *Gladiolus*, and *Freesia*. Most of them perennate by means of corms (*Crocus*, p. 80, Fig. 56), or sympodial rhizomes (many species of *Iris*). The leaves are often equitant and isobilateral, e.g. *Iris*.

The **inflorescences** are usually small cymes variously arranged. Thus in *Iris* the flowering axis ends in a flower (which opens first), and has small lateral cymes each invested by a spathe. In *Gladiolus* and *Freesia* the lateral cymes are reduced to single flowers, each with a spathe (bract), so that the inflorescence is like a spike. In some species of *Crocus* the flowering axis ends in several flowers (cyme); but in the common species it is one-flowered (cf. Amaryllidaceae).

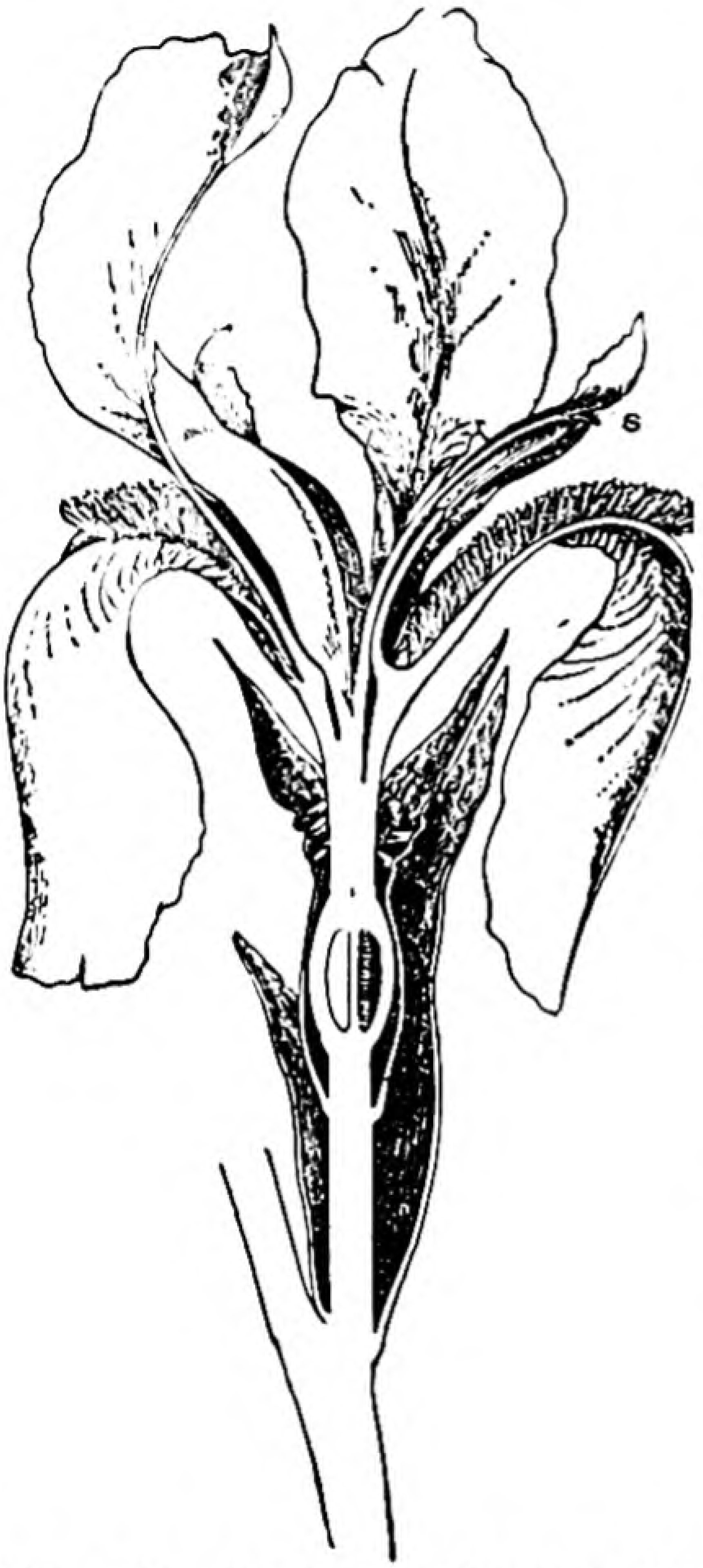

Fig. 228. VERTICAL SECTION OF FLOWER OF *Iris*. (AFTER CHURCH.)

On the left are shown an outer perianth segment, a petaloid style entire, and an inner posterior perianth segment cut in half. On the right an outer anterior perianth segment and a style are cut in half showing a stamen lying between them; at the back is a lateral inner perianth segment (petal); s = stigma; bract and bracteoles are also shown.

The **flowers** (Fig. 228) are hermaphrodite, regular (*Iris* and *Crocus*), or zygomorphic (*Gladiolus*, *Freesia*), epigynous. **Perianth** of six segments in two series, gamophyllous, petaloid, superior.

Androecium of three epiphyllous stamens; they represent the outer whorl, the inner whorl being suppressed, and are situated between the carpels and the outer perianth segments. The anthers are extrorse and lie on the outer side of the styles. **Gynaeceum** tricarpellary, syncarpous; ovary inferior, trilocular, with ∞ anatropous ovules; placentation axile. The styles are united below, but free above, and sometimes expand into three large petaloid lobes (*Iris*). **Fruit** a loculicidal capsule. **Seed** endospermous.

Floral formula:

$$\overparen{P(3+3)\,A}3 + 0\,G(\bar{3}).$$

In *Crocus* nectar is secreted by a nectary on top of the ovary (which is at first underground), and rises to the mouth of the long slender perianth tube. The flowers are protandrous, and are pollinated by bees or butterflies, which touch the stigmas before the anthers. Failing cross-pollination, self-pollination may occur. In *Iris* (see Fig. 228) the anthers and pollen are protected by the petaloid styles. The stigmas are three thin membranes developed on the outer surfaces of the styles just above the anthers. Nectar is secreted by the tissue of the basal portion of the perianth tube. A bee on entering the flower first pushes against the upper surface of the stigma, which alone is receptive, and then brushes the extrorse anthers. It is guided in many species by broad bands of hairs developed on the perianth segments.

The Indian Iridaceae are mainly found in Kashmir where many species of *Iris* are cultivated or grow wild, and form a notable feature of the landscape along with *Crocus sativus*, the saffron or kesar.

Apart from the species which are cultivated as ornamental plants, few are of economic importance. Orris root, which smells like violets and is used in perfumery, is the dried rhizome of *Iris florentina*. The stigmas of *Crocus sativus* constitute saffron.

F. ORDER SCITAMINEAE.—Flowers cyclic, homoiochlamydeous or heterochlamydeous, 3-merous, typically diplostemonous, frequently with reduction of the androecium to only one stamen, rarely actinomorphic, usually zygomorphic. Ovary inferior, usually 3-locular with large ovules. Seeds usually with an arillus and with both perisperm and endosperm.

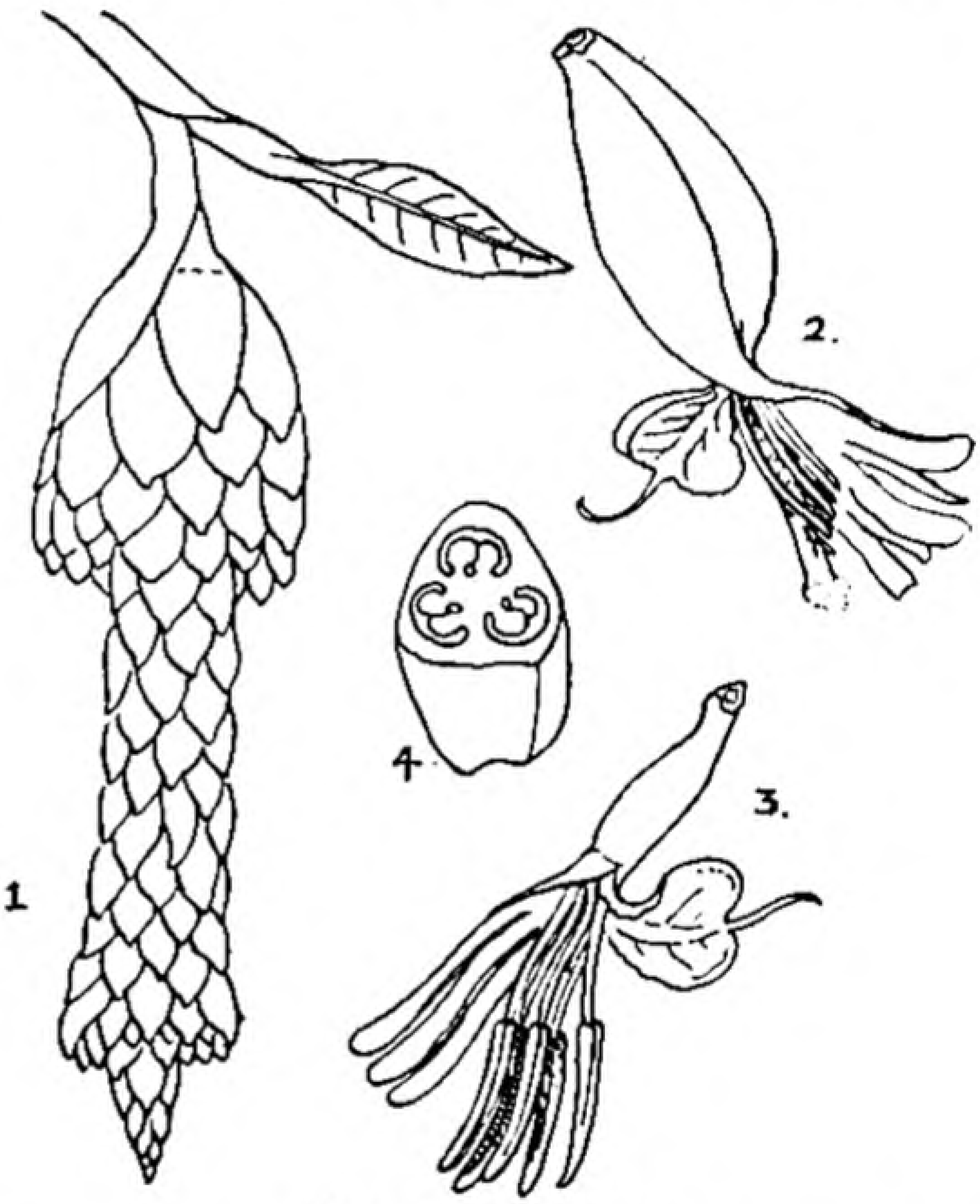

Fig. 229. *Musa*.

1, Inflorescence; **2**, Female flower; **3**, Male flower; **4**, Ovary cut transversely.

FAMILY **Musaceae.**—Flowers as above, hermaphrodite or unisexual, zygomorphic. Perianth more or less petaloid, frequently differentiated, stamens usually only 5 fertile and the sixth staminodal, stigma 3–6 lobed. Ovary 3-locular, 1–∞ ovules per loculus. Fruit a berry or capsule. Seeds frequently with arillus. Endosperm and perisperm. Embryo straight. Usually large herbs with gigantic, oval or oblong leaves. Inflorescence frequently contracted into a spike with large, brightly coloured bracts. Flowers ornithophilous.

This is a small family of some 150 species. The genus *Musa* includes the banana or plantain. *M. paradisiaca* is extensively cultivated for its fruit, and *M. textilis* is occasionally cultivated for its fibre (Manila hemp). The apparent stem is in reality made up of the leaf-bases, rolled one inside the other. The laminae are unicostate (Fig. 102, A) and tend to tear between the veins, making them appear to be pinnately divided. The flowers of *Musa* (Fig. 229) are unisexual, the male above the female in a bracteate spike. 3 sepals and 2 petals form a tube split down one side, and the remaining petal is opposite the split, free. Usually five stamens are perfect, the sixth rudimentary or absent. The inferior ovary of 3 carpels is originally 3-locular. In the wild plantain (*M. superba*) numerous black or brown seeds are developed in a berry which is edible but insipid, but in the cultivated *M. paradisiaca* the ovules abort and so the fruit is seedless.

Another cultivated plant is *Ravenala madagascariensis*, the traveller's tree, which has a true stem. *Strelitzia*, pollinated by birds, and *Heliconia*, are ornamental plants.

G. ORDER MICROSPERMAE.—Flowers cyclic, homoiochlamydeous or heterochlamydeous, trimerous, typically diplostemonous, but frequently with obvious reduction in the androecium. Ovary inferior tri- or uni-locular, with numerous small ovules on the axile or parietal placentae.

FAMILY **Orchidaceae.**—Flowers (Figs. 230-231) homoio- or hetero-chlamydeous, typically trimerous, almost always hermaphrodite, zygomorphic, resupinated. The fertile stamens are either the single anterior stamen of the outer whorl, or the two anterior stamens of the inner whorl. Correspondingly the two anterior stamens of the inner whorl, or the one anterior stamen of the outer whorl may become staminodes. Very rarely are the other stamens developed. Carpels three, syncarpous, sunk in the hollow receptacle. The ovary is prolonged above the insertion of the corolla as a gynostemium and bears the stamen(s). The pollen is massed into pollinia and the microspores remain in tetrads. Stigmas three, on the inner surface of the gynostemium, the anterior are usually rudimentary or forming the rostellum. Ovary inferior, very frequently twisted, usually unilocular with three parietal placentae and numerous ovules. Fruit a capsule with numerous very small seeds without endosperm.

This is a very large and interesting family comprising only herbs perennating by means of rhizomes, tubers (Fig. 89), etc. They are of very diverse habit, including land-plants, epiphytes (p. 153), saprophytes, etc. Many of the land and epiphytic forms are adapted to xerophytic conditions (p. 166), storing up water and reserves either in thickened internodes called *pseudo-bulbs* or in fleshy leaves.

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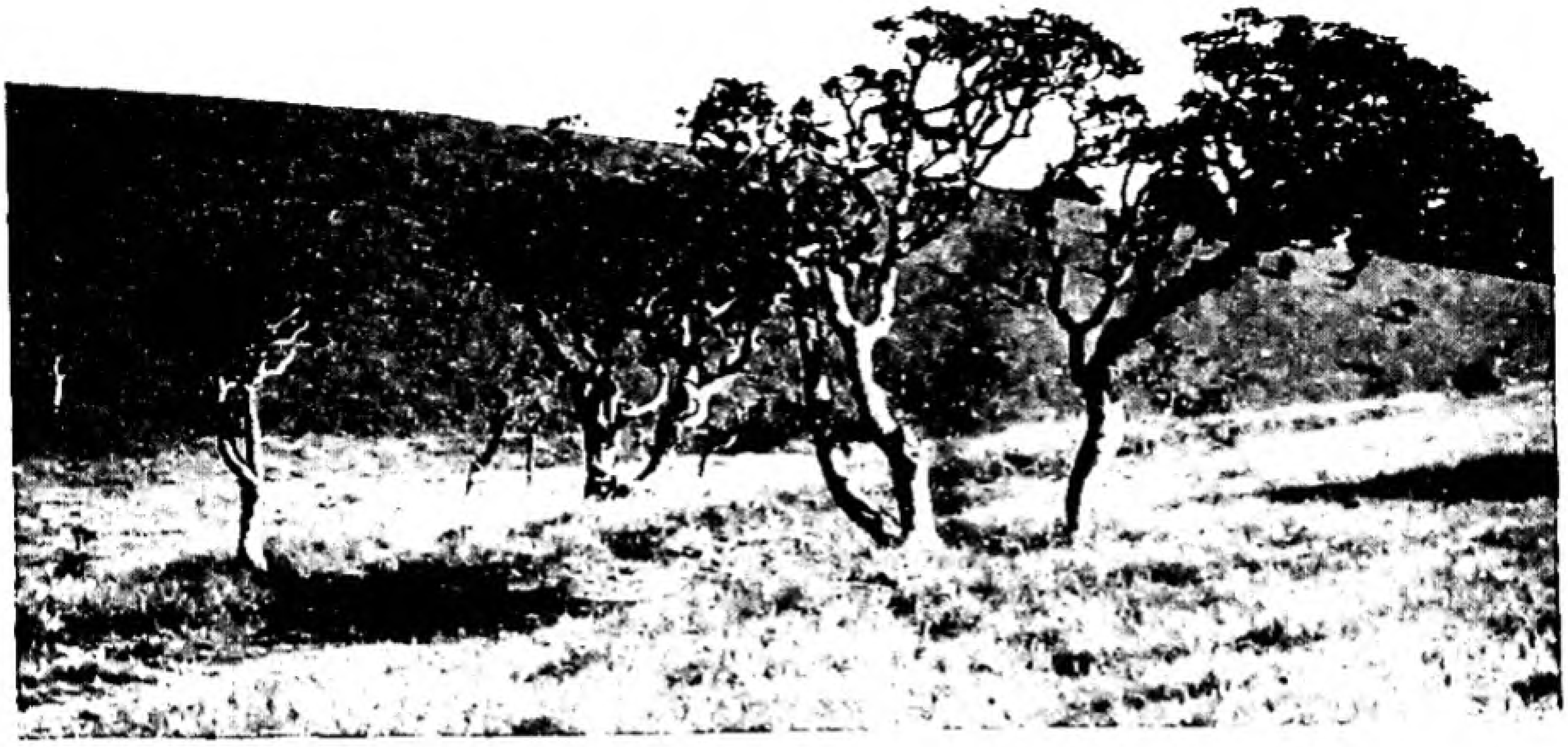

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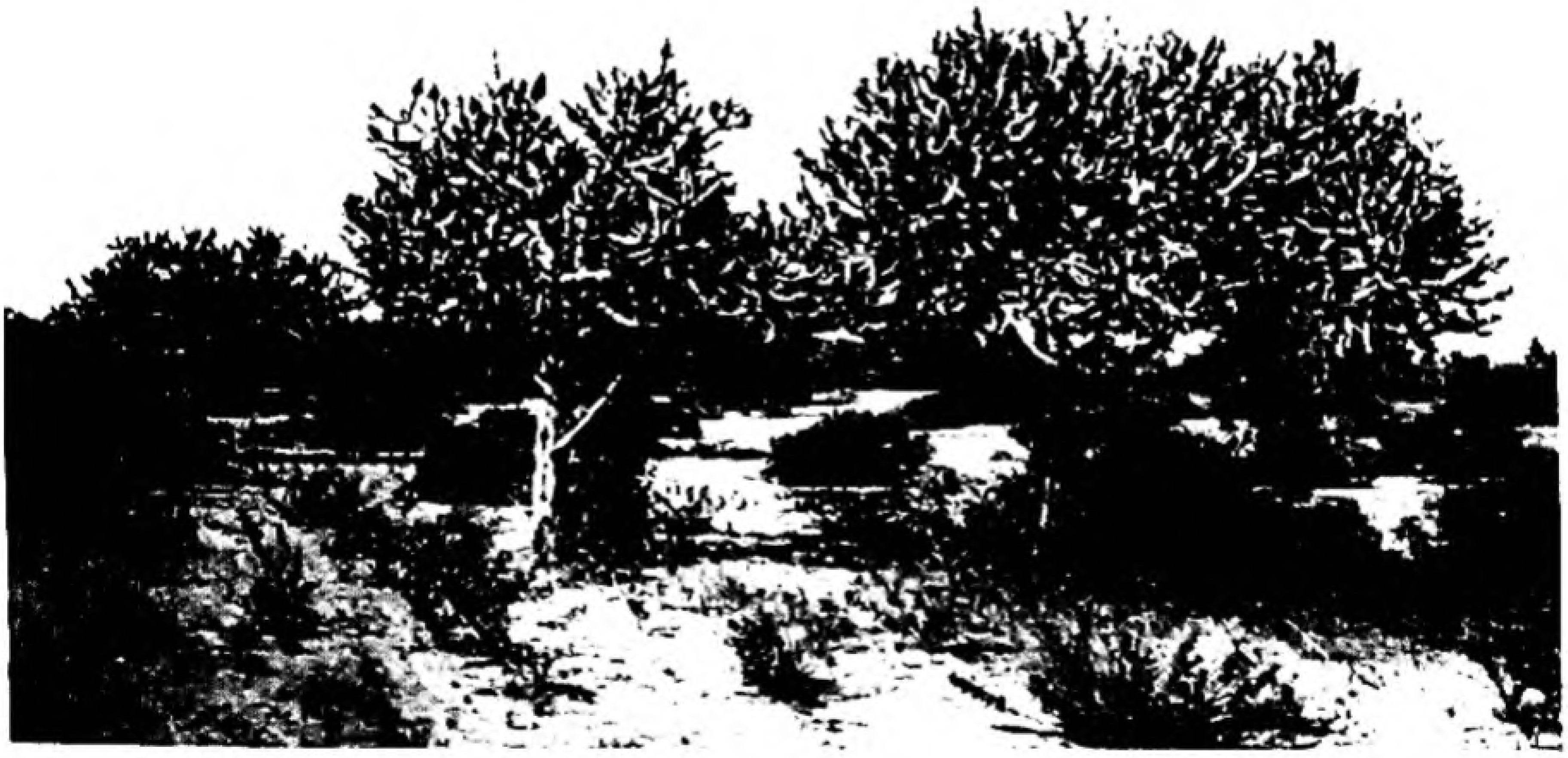

Photos N.G.B.

PLATE VII

1. Horton Plains, Ceylon.
Rhododendron arboreum on patanas at altitude of about 7,000 ft.

2. Xerophytic Vegetation on East Coast of Ceylon.
The trees are *Euphorbia antiquorum*.

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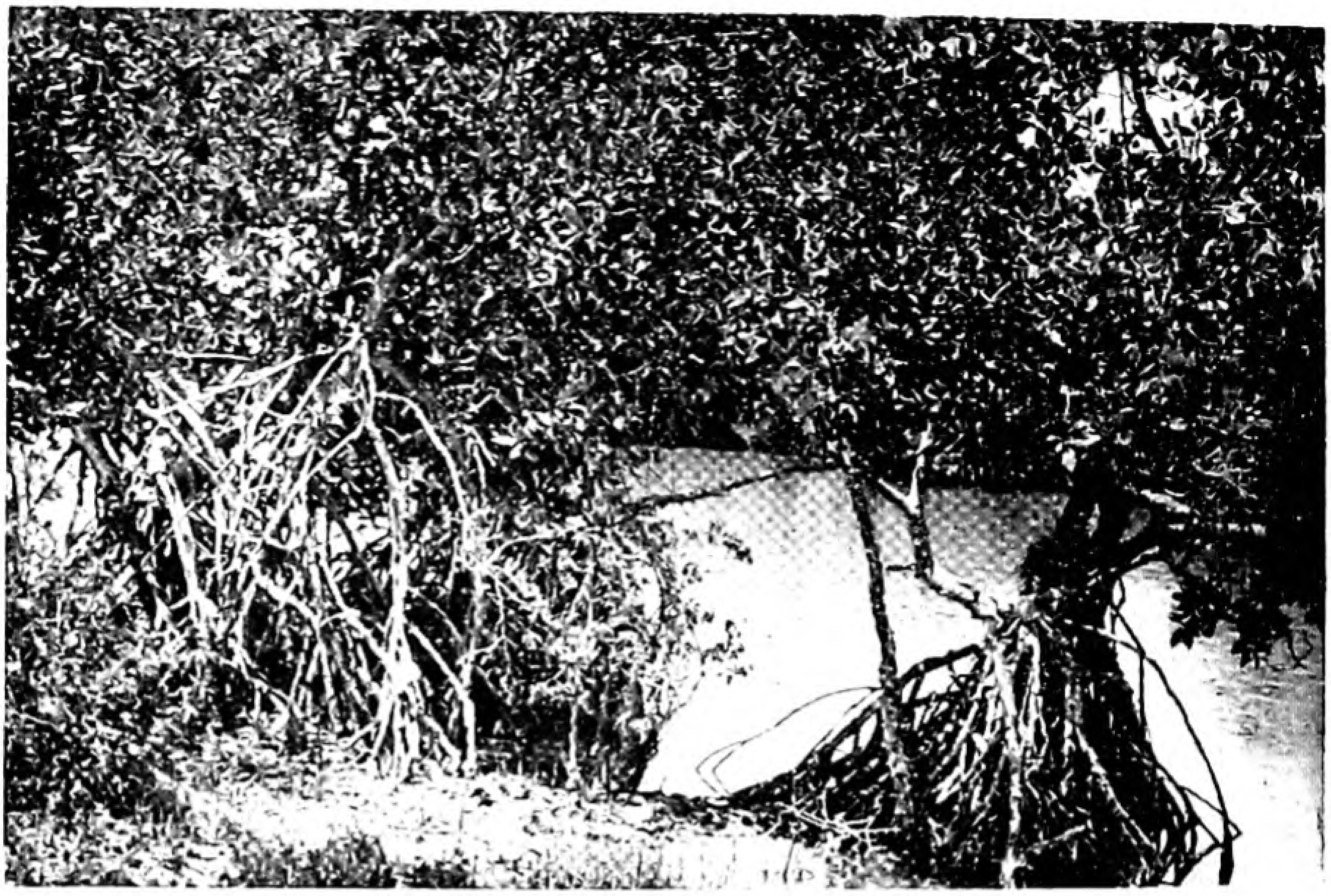

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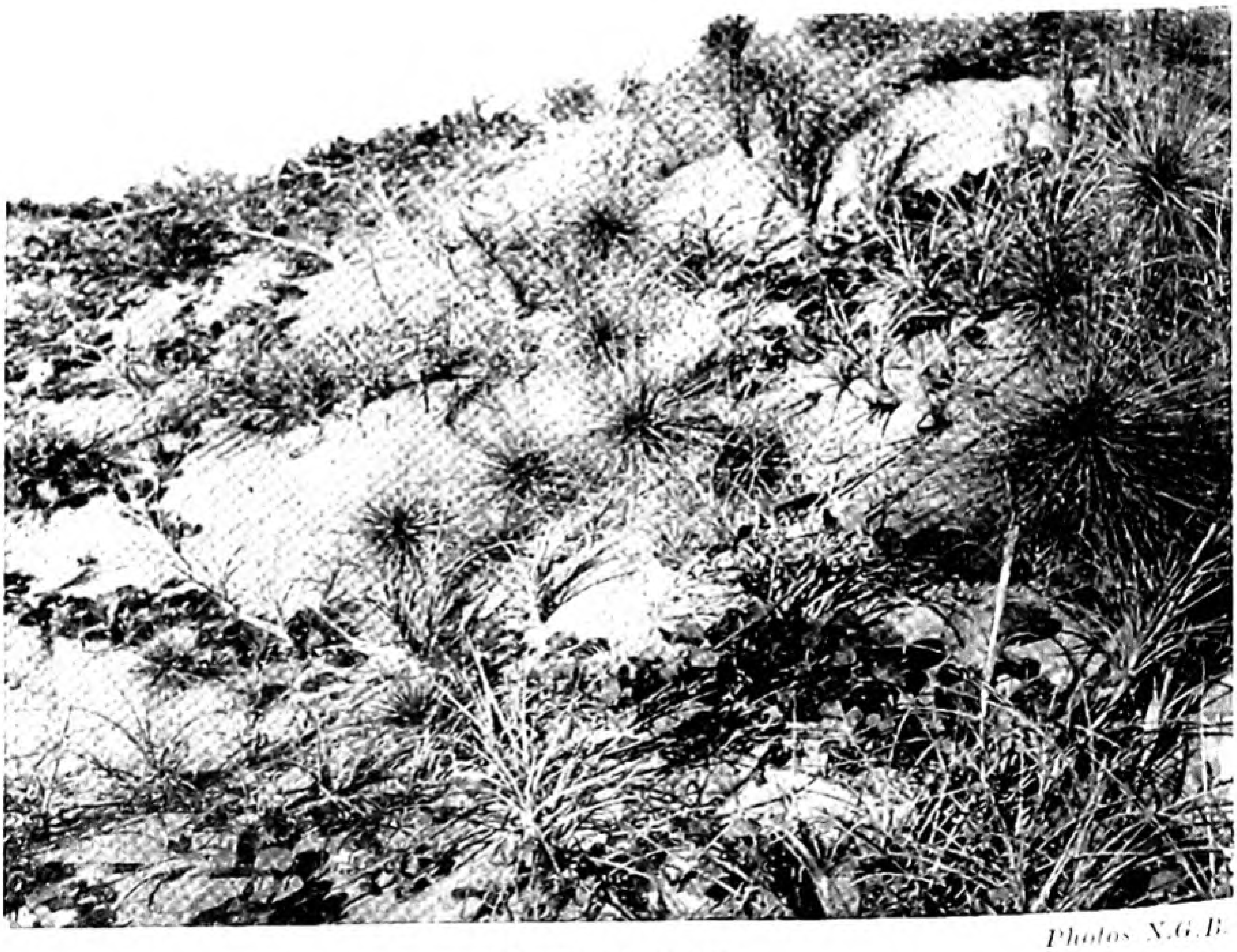

Photos N.G.B.

PLATE VIII

1. MANGROVE SWAMP WITH *Rhizophora mucronata*.
In the foreground can be seen some of the upright pneumatophores of *Avicennia*.

2. SAND-DUNES WITH *Ipomoea pes-caprae* AND *Spinifex littoreus*.
The large, spiny fruiting heads of the latter are conspicuous.

The epiphytic orchids which abound in the tropics are especially interesting. They support themselves by means of clinging adventitious roots, on which are developed absorbing roots. The latter penetrate into the humus which collects between the clinging roots and the support. Then there are the aerial roots, each of which has a spongy sheath of reticulately thickened cells, perforated between the thickenings, called the *velamen* (Fig. 121). The velamen rapidly absorbs drops of water which fall on it. The production of abundant small seeds easily carried by the wind may be correlated with the epiphytic habit.

The **inflorescence** is racemose, most frequently a spike. The **flowers** (Figs. 230 and 231) may be compared with the typical monocotyledonous form, the many striking differences met with being due to suppression, adhesion, and hypertrophy of certain parts.

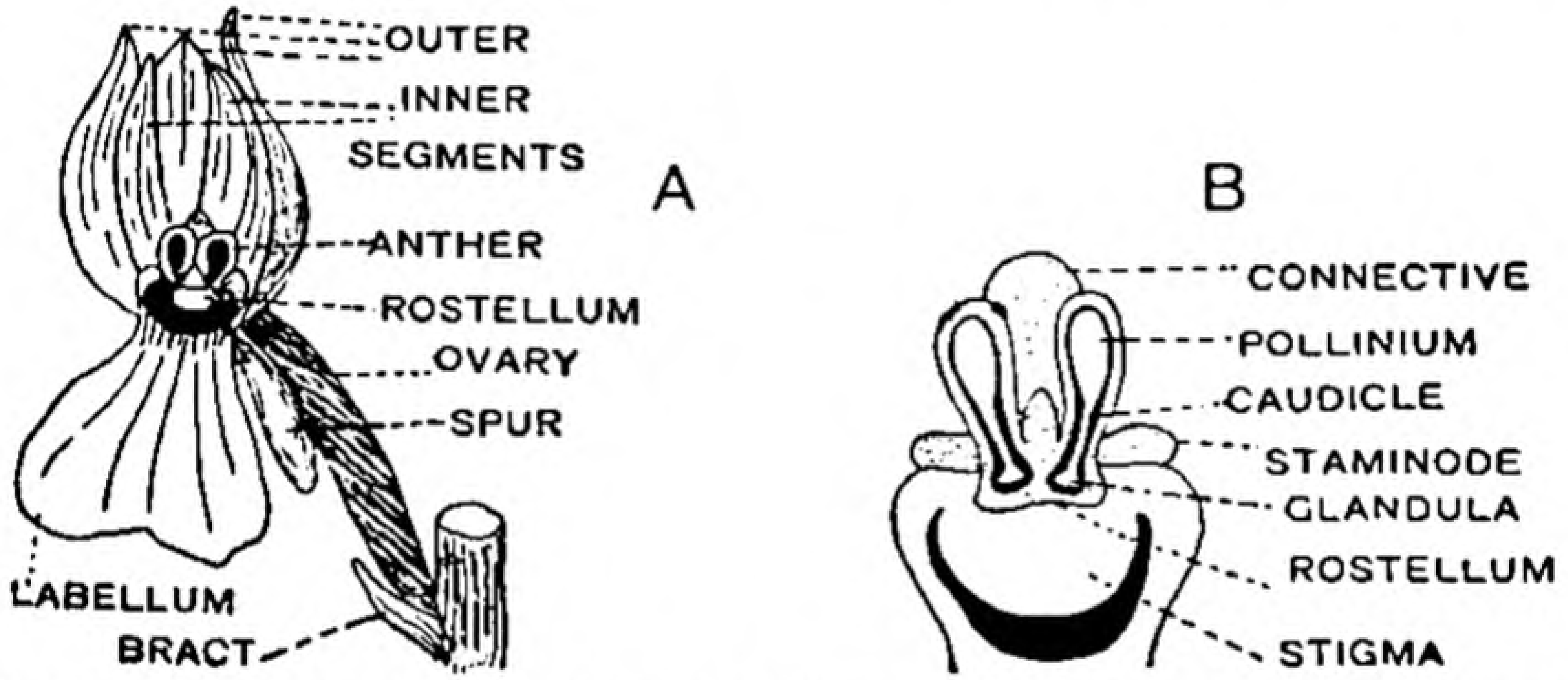

Fig. 230. A, FLOWER OF *Orchis*; B, CENTRAL PART OF THE SAME, PERIANTH SEGMENTS REMOVED.

The **perianth** is petaloid, zygomorphic, and consists of six segments in two whorls. The posterior segment of the inner whorl is always more strongly developed than the others; it forms the *labellum*. Owing to the twisting of the inferior ovary, the labellum comes to be anterior (the *resupinate* condition) and serves as the landing-stage for the insect. In the genera *Orchis*, *Calanthe*, *Vanda*, *Saccolabium* and *Habenaria* the labellum is spurred.

The **androecium** usually consists of one stamen and two staminodes (e.g. *Orchis*), but in *Cypripedium* and its allies there are two stamens and one staminode. Corresponding to this there are two divisions of the Orchidaceae—the *Monandrae* and the *Diandrae*. The stamens are fused with a prolongation of the axis of the flower called the **gynostemium** (or column), which also bears the three stigmas on its apex (the *gynandrous* condition, p. 239). In the majority of the Orchidaceae the microspores are united into *pollinia*.

The **pistil** is tricarpellary and syncarpous; the ovary inferior and unilocular, except in *Apostasia* where it is 3-locular. The ovules do not develop until after pollination; they are anatropous, and borne on three parietal placentas. The fruit is a capsule containing an enormous number of very small, light seeds. The seed is non-endospermous, and its embryo is not differentiated into plumule, radicle, and cotyledon.

In *Orchis* (e.g. *O. mascula*) which may be taken as a type of the *Monandrae*, the single fertile stamen is the anterior one of the outer whorl; the two staminodes are the anterior ones of the inner whorl (Fig. 231). Two pollinia are present. One of the stigmatic surfaces is incapable of being pollinated, and develops into a projecting structure called the **rostellum** (Fig. 230). The microspores are held together by delicate threads which run together at the base of the anther-lobe to form a mucilaginous cord called the **caudicle**, which is attached below to a sticky disc (Fig. 183, C), in contact with the rostellum. The two functional stigmatic surfaces are below the rostellum, the two anther-lobes above it, one on each side, each containing a pollinium. These various structures are borne on the gynostemium.

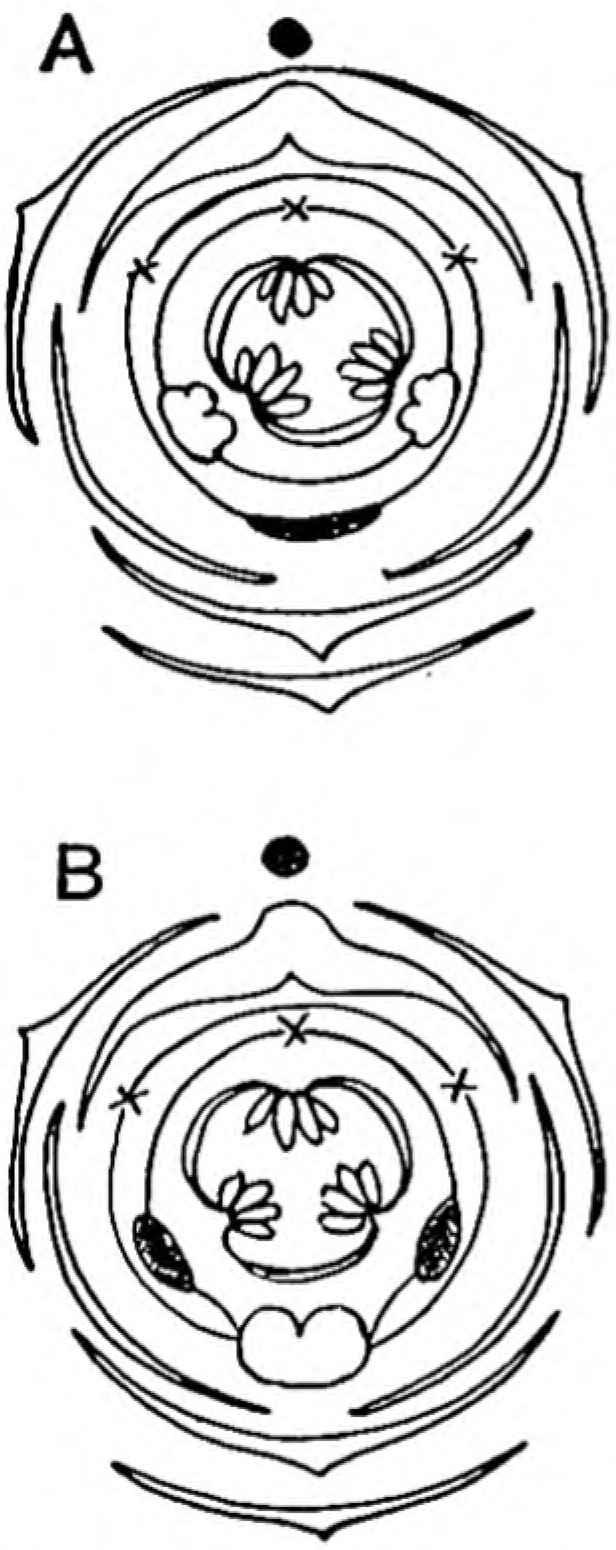

Fig. 231. Floral Diagram of A, *Cypripedium*, B, *Orchis*.

In *Cypripedium* (Fig. 231) the two stamens are the anterior ones of the inner whorl, *i.e.* those represented by staminodes in *Orchis*. The staminode is the anterior one of the outer whorl, *i.e.* the fertile one in *Orchis*. There is no rostellum. The three stigmas are fused in one. The microspores are not aggregated into pollinia, but are sticky.

The flower is often more complex than we have here described. Outgrowths of the summit of the receptacle may make the other perianth leaves appear to spring from the labellum.

Pollination.—The flowers are entomophilous. No nectar is secreted; the insects have to pierce the tissues to get it. The pollination contrivances in Orchidaceae are innumerable and in many cases extraordinary. We may consider *Orchis* as an example. The insect alights on the labellum, and seeks in the spur of the labellum for the nectar. The head of the insect comes in contact with the rostellum, and pushes aside the membrane covering the sticky discs of the caudicles so that the insect presses against them. While the insect is piercing the spur, the mucilaginous substance of the discs "sets," and when the insect leaves the flower the pollinia are dragged out. At first they stand erect on the back of the head of the insect, but very gradually they are bent forward, owing to hygroscopic properties which their stalks possess, so that when the insect enters another flower they touch and are held by the sticky stigmas.

Floral formulae: *Orchis*—$P3 + 3\ A1\ G(\bar{3})$.
Cypripedium—$P3 + 3\ A2\ G(\bar{3})$.

This family is well represented in the flora of India, but the majority of species are found in the hills. *Zeuxine sulcata* (= *Z. strateumatica*) is one of those well distributed in the plains. In the north-west Himalaya the orchids are mostly terrestrial, while epiphytic species preponderate in the eastern Himalaya. Species of *Dendrobium*, *Coelogyne* and *Vanda* are epiphytes; *Vanilla*, *Spiranthes*, *Epipactis*, *Calanthe* and *Habenaria* are terrestrial. A few are leafless saprophytes without chlorophyll, e.g. *Epipogum*, *Neottia*.

Some species of *Habenaria* have spurs several inches long. *Spiranthes* is commonly called lady's tresses on account of its spirally twisted inflorescence, and *Cypripedium*, lady's slipper, because of the shape of the labellum. *Satyrium* has two spurs.

The only orchid of any economic importance, apart from the numerous species which are cultivated for their flowers, is *Vanilla planifolia*, whose pods, collected and dried, form the vanilla of commerce.

5. Families of Dicotyledons

SUB-CLASS I, ARCHICHLAMYDEAE

A. ORDER FAGALES.—Flowers cyclic, homoiochlamydeous, appearing haplochlamydeous, rarely naked, usually unisexual, monoecious. Stamens generally opposite the perianth leaves. Ovary inferior. Carpels (2–6), each with 1–2 ovules. Fruit usually a nut containing one seed, non-endospermous.

1. FAMILY **Betulaceae.**—Flowers unisexual, monoecious. Perianth homoiochlamydeous, appearing haplochlamydeous, free or fused, or absent. Male flowers, 2–10 stamens with usually divided anthers. Female flowers (2), two stigmas. Ovary inferior, at the base bilocular, with 2 pendulous, anatropous ovules with one integument. Examples: birch (*Betula*), alder (*Alnus*), hazel (*Corylus*), hornbeam (*Carpinus*).

2. Family **Fagaceae.**—Flowers usually unisexual, rarely hermaphrodite. Perianth haplochlamydeous, 4–7 perianth leaves, bract-like, united. Male flowers with 4–14 stamens. Female flowers with (3) rarely (6) carpels. Stigmas 3. Ovary inferior, 3-locular, each with 2 pendulous ovules with 2 integuments. Fruits single or grouped in a cupule; each fruit 1-seeded, endosperm absent. Examples: oak (*Quercus*), beech (*Fagus*), sweet chestnut (*Castanea*).

It is convenient to treat these two families together. They are widely distributed in temperate regions and consist of trees and shrubs with simple, alternate, stipulate leaves.

The **inflorescences** are called catkins (p. 255). The female catkins are not pendulous. The *typical* **catkin** consists of an elongated pendulous axis bearing numerous small spirally arranged bracts (b), in the axil of each of which are three flowers representing a sessile or reduced dichasium. The terminal (middle) flower has two lateral bracteoles (α and β), and in the axils of these arise the two lateral flowers, which also may have bracteoles (α', β'). Thus there are typically three flowers and six bracteoles in the axil of each bract (Fig. 232). From this it is evident that the catkins characteristic of the order are mixed inflorescences, *i.e.* spikes of dichasia (see p. 256).

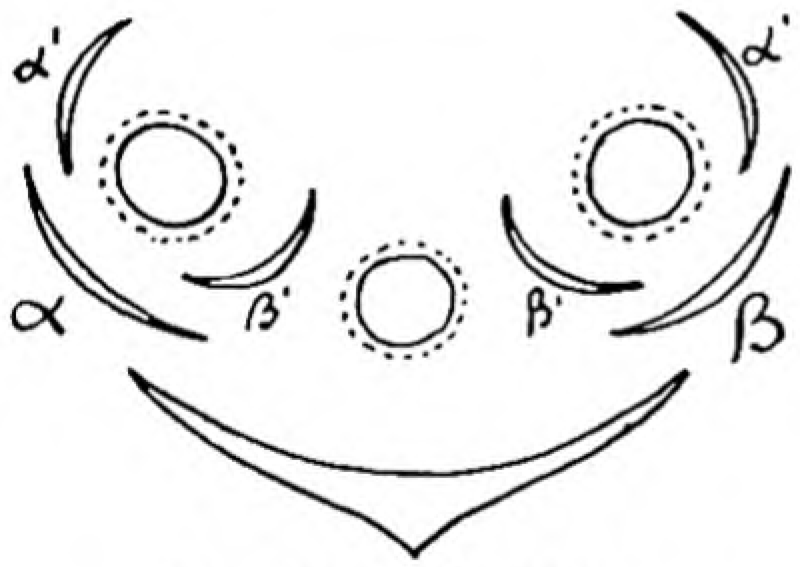

Fig. 232. Fagales.
Floral diagram.

The typical form, however, is departed from, more or less, in the various genera. There may be more than three flowers. Sometimes only the middle flower or only the two lateral flowers are present, and some or even all of the bracteoles may be absent. The whole inflorescence is, in some cases, reduced to a cluster of flowers. The various modifications are described below. The female catkins persist till the fruits are ripe, or even longer as in the alder.

The **flowers** are unisexual, monoecious, and borne (with rare exceptions—e.g. sometimes in chestnut) in different catkins. They are anemophilous and, in correlation with this, they frequently come out before the leaves (hazel and alder), or just when the leaves are unfolding (birch and oak). A **perianth** is sometimes present, and occasionally well developed; when present it is epigynous.

The **stamens** are two, four, or more; sometimes they are split or forked (Figs. 234 and 237, c). The **gynaeceum** is bicarpellary (Betulaceae), or tricarpellary (Fagaceae), syncarpous; the ovary, at the time of fertilisation, bi- or tri-locular, inferior; ovules, one

(Betulaceae) or two (Fagaceae) in each loculus, anatropous and usually pendulous.

The **fruit** is dry, indehiscent, one-seeded—a nut or nutlet. In the birch it has a membranous wing and is a samara (Fig. 235, B). The fruits may be liberated from the coherent bract and bracteoles (alder and birch), or these may enclose one or more fruits as a cupule (membranous in hazel and hornbeam, woody in oak and beech). The seed is non-endospermous (Fig. 240).

The following notes indicate the special characters of the various genera:—

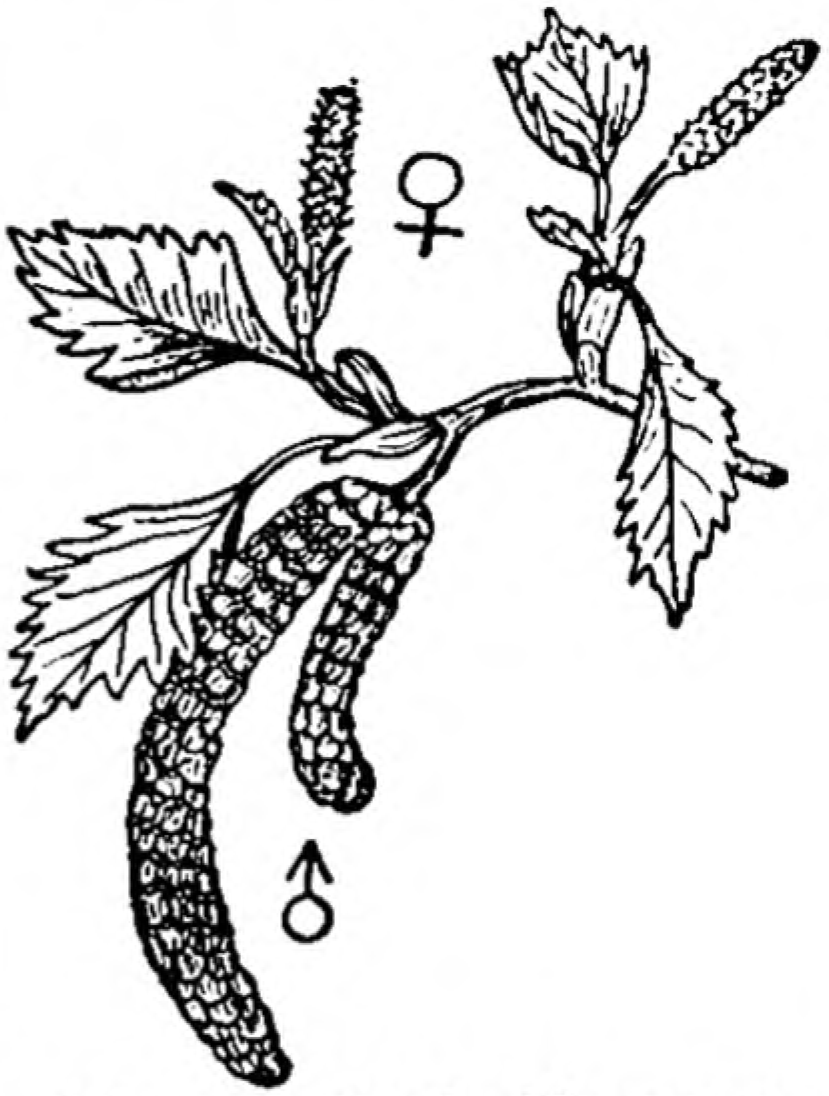

Fig. 233. *Betula*, MALE AND FEMALE CATKINS.

Betula (Figs. 233-235).—The male catkins appear in autumn at the ends of the shoots and are pendulous; the female catkins are borne on short lateral branches which are developed in spring and are erect. Flowering takes place in the Spring. In both catkins each bract has three flowers. Only the two lateral bracteoles are present. Each male flower has a small perianth usually two-lobed, and two stamens the filaments of which are so deeply split that there appear to be four stamens. The female flower has no perianth. The pistil is bicarpellary and has two styles. The fruits are samaras. Bract and bracteoles become fused owing to continued basal growth. The three-lobed scale which they form falls off at fruiting, but does not invest the fruits. *Betula pendula* is the white- or silver-birch, *B. pubescens* the birch.

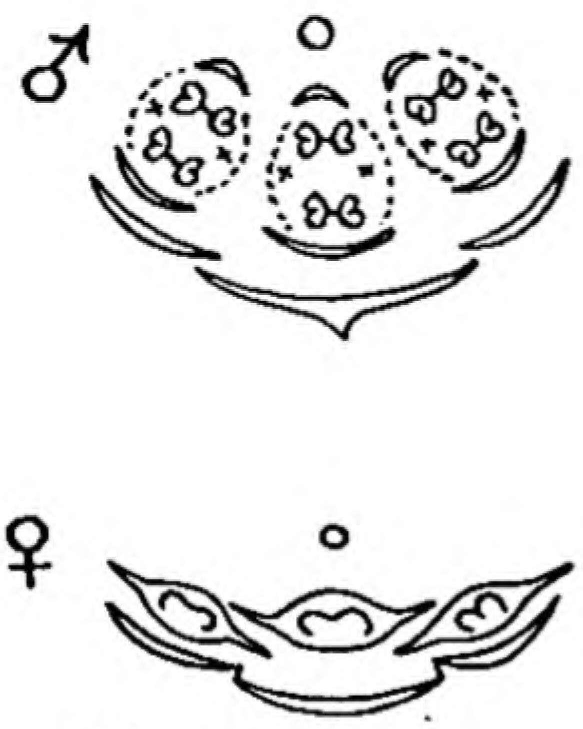

Fig. 234. *Betula.*
Diagram of Dichasia in male and female catkin.

Alnus.—The male catkins are elongated; the female small and somewhat ovoid. Both appear in autumn, and are more or less erect. Flowering takes place in the Spring. Each bract of the male catkin has three flowers, but in the female only the lateral flowers are developed. There are four bracteoles, α, β, α', β'. The ♂ flower has a four-lobed perianth and four stamens opposite the lobes. The ♀ flower resembles that of the birch. The female catkins, including the hard five-lobed scales formed from the bracts and bracteoles remain on the tree after the fruits are set free. The fruits are not winged (nutlets). *Alnus glutinosa* is the alder.

Corylus (Figs. 236-240).—The catkins appear in autumn. The pendulous male catkins are borne 1-3 together on a short axillary shoot. The female are solitary, axillary, and are not distinguishable from foliage buds till the spring when flowering takes place and the crimson styles protrude at the top. In the male only the median flower and the α and β bracteoles are developed in each bract. The flower has four deeply-split stamens and there is no perianth. In the female catkin the lower bracts are sterile; in the upper fertile bracts *all* the bracteoles (α, β, α′, β′) but only the lateral flowers are present. Each female flower has a minute, toothed, greenish perianth on the top of the ovary; there are two styles. The two bracteoles of each flower with one of the lateral bracteoles (α, α′, β′; β, α′, β′) fuse, owing to continued basal growth, to form an involucre which develops into the membranous cupule (husk—Fig. 239). *Corylus Avellana* is the hazel.

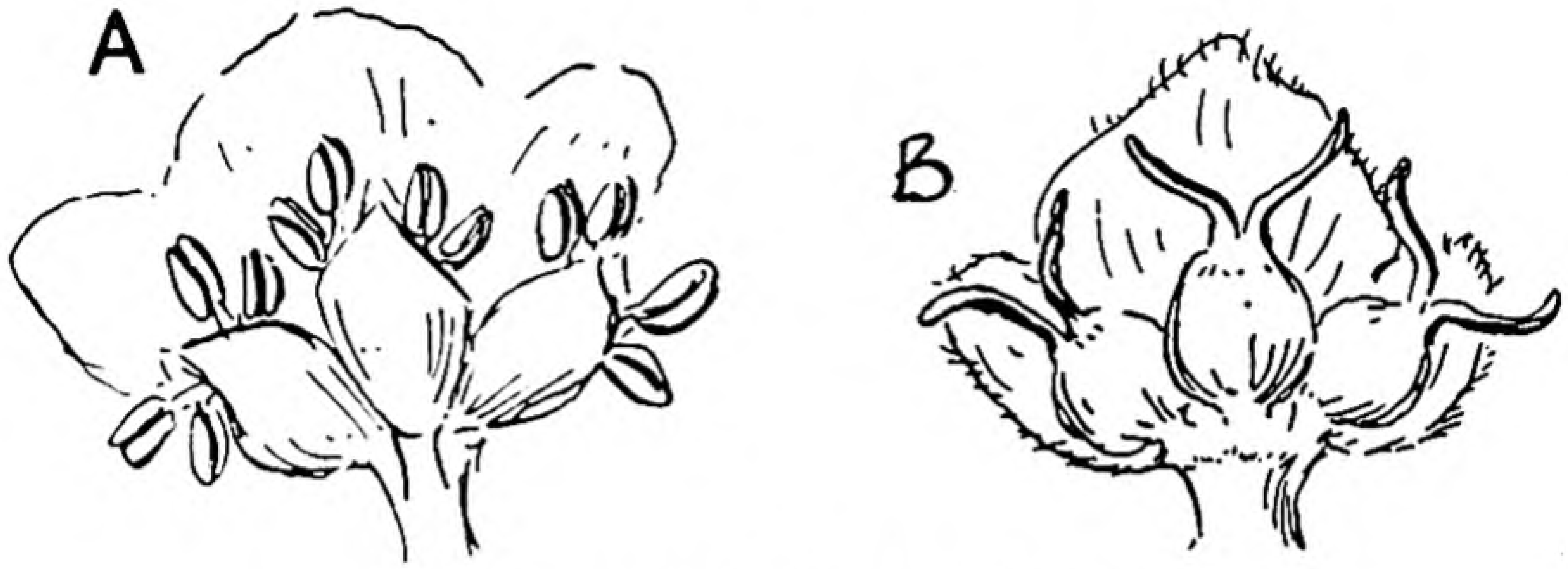

Fig. 235. *Betula*, Dichasia Dissected.
A, Male; B, Female.

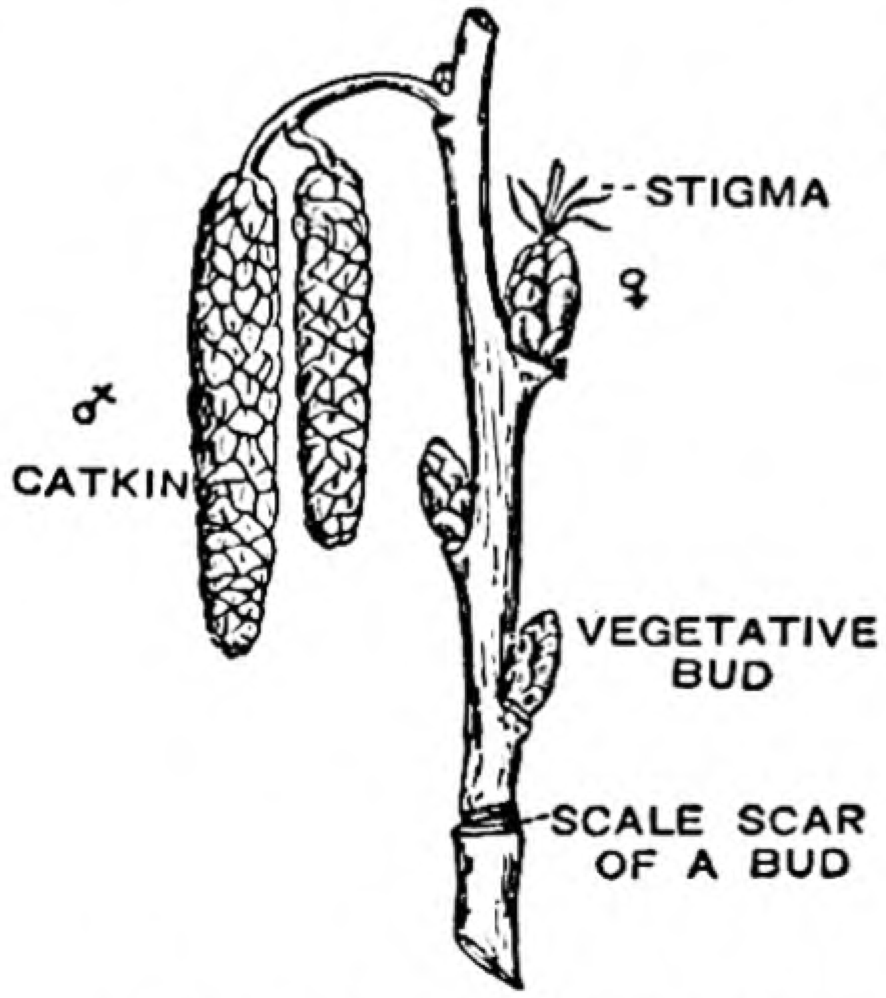

Fig. 236. *Corylus*, Male and Female Catkins.

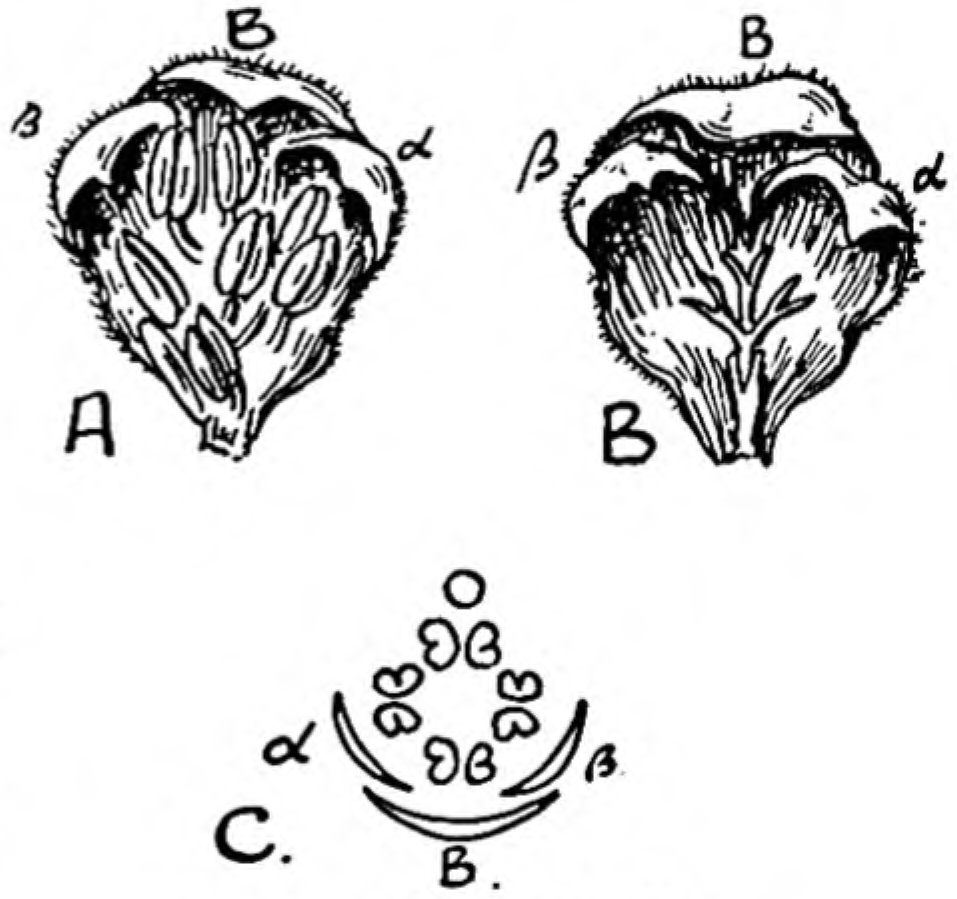

Fig. 237. *Corylus*.
A, Male flower with bract and two bracteoles;
B, ditto, with anthers removed;
C, Floral diagram.

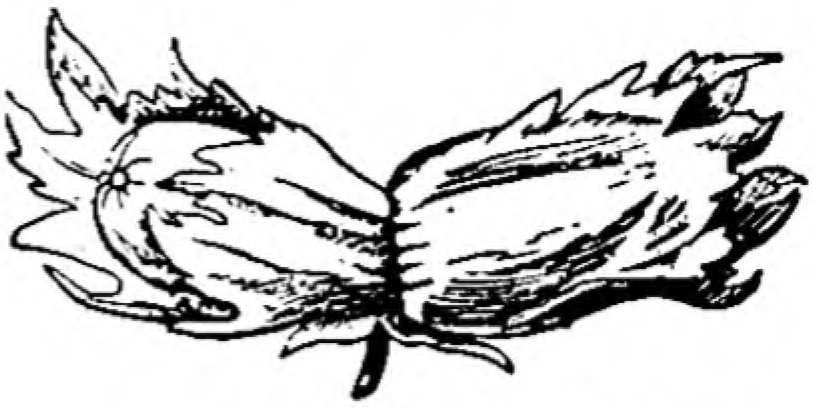

Fig. 239. *Corylus*, NUTS.

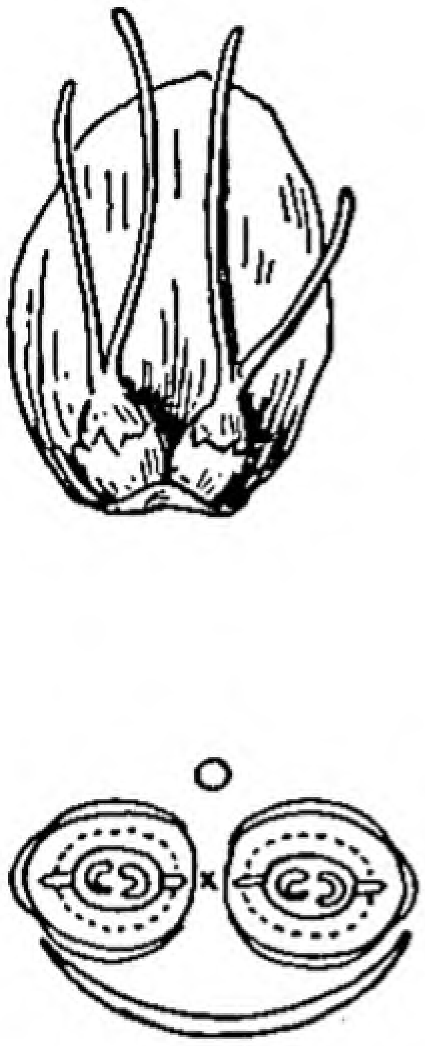

Fig. 238. *Corylus*. DISSECTION AND DIAGRAM OF ♀ DICHASIUM.

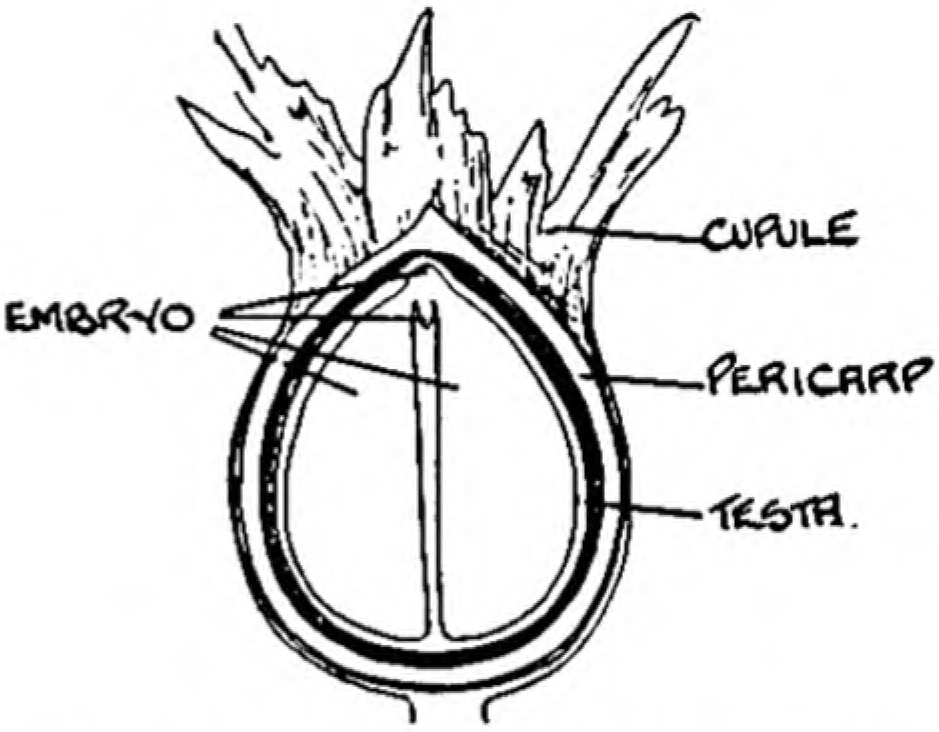

Fig. 240. *Corylus*. LONGITUDINAL SECTION OF NUT.

Carpinus.—The flowers are similar to those of the hazel, but in the male catkins there are no bracteoles and each bract has 4-10 divided stamens. The cupule is large and trilobed (Fig. 241); the centre lobe is formed from the bracteole α or β, the lateral lobes from α' β'. It aids in wind-dispersal. *Carpinus Betulus* is the hornbeam.

Quercus (Fig. 244).—The catkins appear in the spring, the male in the axils of bud-scales, the female in the axils of foliage leaves. Flowering occurs in the spring. The male catkin here is a long slender and pendulous spike, the flowers being borne singly in the axils of the bracts. They represent the median flowers and there are no bracteoles. Each (Fig. 242, c) consists of a perianth of a varying number of bract-like segments (4-7) and as many or more stamens (frequently 10). A rudimentary ovary may be present.

The female catkin contains only 2 or 3 flowers which may be in a cluster (*Q. sessiliflora* = *Q. petraea*) or may be separated by the elongation of the peduncle (*Quercus Robur*). They are borne in the axils of bracts and represent the median flowers (in some allied species

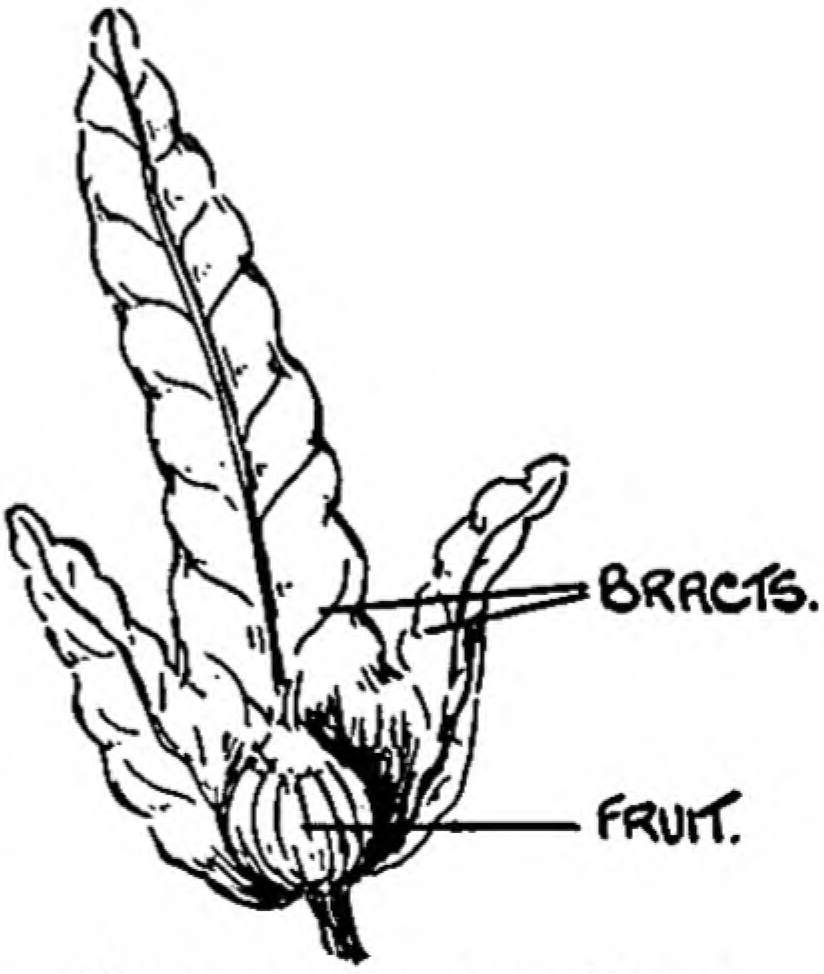

Fig 241. *Carpinus* FRUIT.

all three flowers are present). Each has an epigynous 3-8 toothed perianth and is surrounded by a number of imbricate scales forming an involucre which afterwards develops into the acorn cup (cupule). The involucre is regarded by some as representing the four bracteoles of the lateral flowers. The ovary is trilocular, and each loculus has two pendulous anatropous ovules, but only one loculus and one ovule develop. The fruit (acorn) is a nut seated in a cup-shaped cupule. *Quercus Ilex* is the holm- or evergreen-oak; *Q. Suber*, the cork oak, *Q. Cerris*, the Turkey oak.

Fagus (Fig. 243).—The catkins are developed in spring in the axils of foliage leaves. The male is really a clustered dichasial cyme of about twelve flowers borne on an elongated pendulous peduncle. The flowers are shortly stalked and have a 4-7 lobed perianth, and from 8 to 12 stamens. There are no bracts. The female catkin is stalked, erect, and consists of only two flowers (dichasial cluster) enclosed in a fleshy, four-lobed involucre (cupule), and a number of smaller outer scales. The homologies of these parts have not been clearly made out. The flowers themselves resemble those of the oak. The cupule is spiny and resembles a capsule. It contains two triangular nuts (" beech mast ") and separates into four valves.

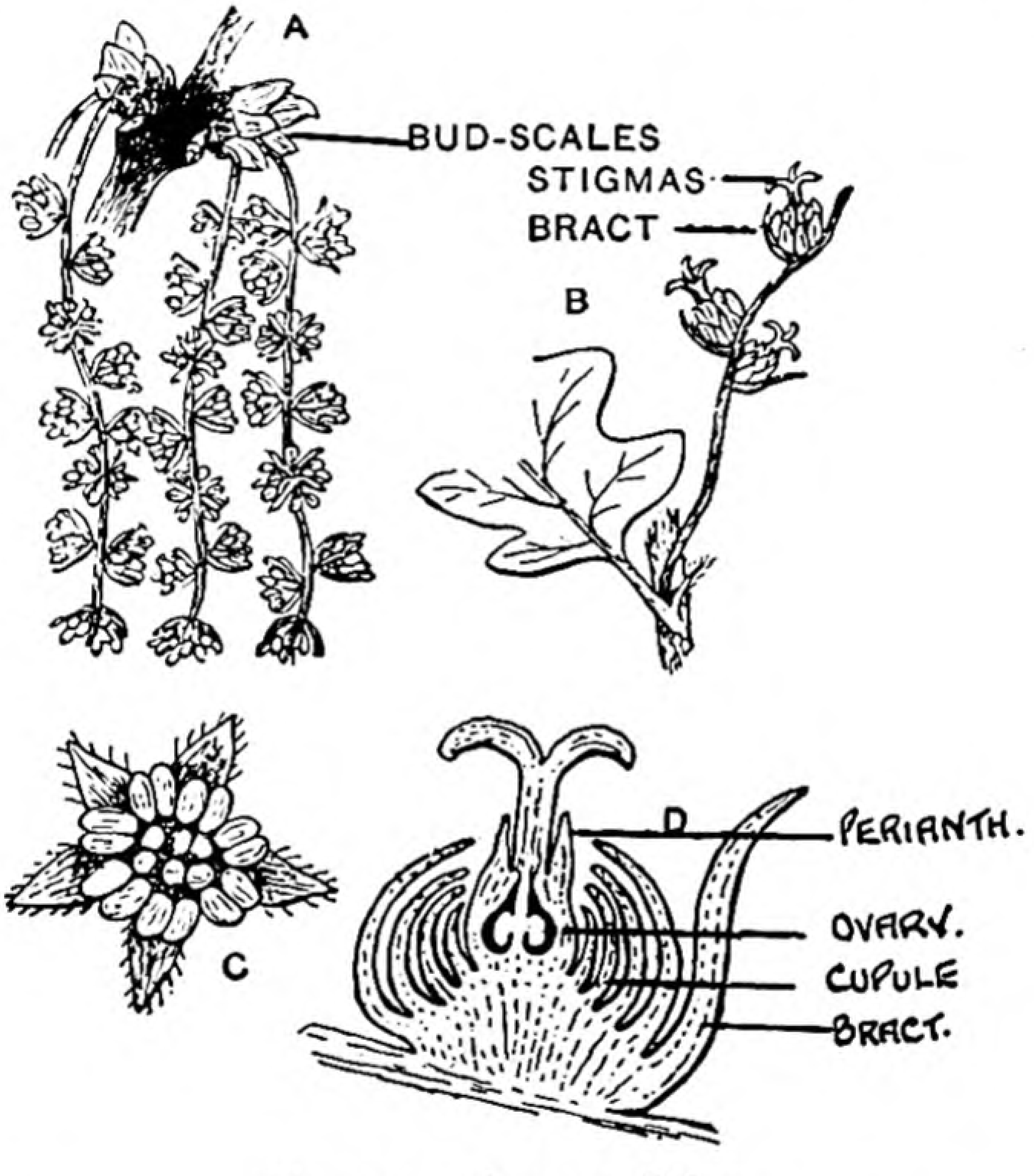

Fig. 242. *Quercus Robur*.
A, Male; B, Female inflorescences; C, Male flower; D, Female flower in section.

Castanea.—The catkins are axillary, and bract and bracteoles are all present. There are usually seven male flowers in the axil of the bract owing to the bracteoles of the lateral flowers also having flowers. The female bracts bear three flowers and the cupule is formed by the four bracteoles of the lateral flowers. The mature cupule is spiny. It contains three nuts and separates into four valves. Frequently catkins are found bearing staminate flowers above and pistillate flowers below. *Castanea sativa* is the sweet chestnut.

The fossil records indicate that plants allied to the living species of the order Fagales occurred as far back in time as the Cretaceous period. The "primitiveness" of their floral characters is a matter of doubt, and their position in a phylogenetic system of classification depends on the interpretation of their floral morphology. The apparent simplicity of this *may* represent a "primitive" condition, but, on the other hand, may be the result of reduction from a less simple condition. We have already referred to the flower as a shoot whose leaves have become modified and assumed reproductive functions. On this interpretation of floral morphology the "primitive" type would have free spirally arranged floral parts, and hermaphrodite flowers. Hence, the absence of a perianth, unisexuality, and syncarpy would represent a reduced state. (See Chap. XVII.)

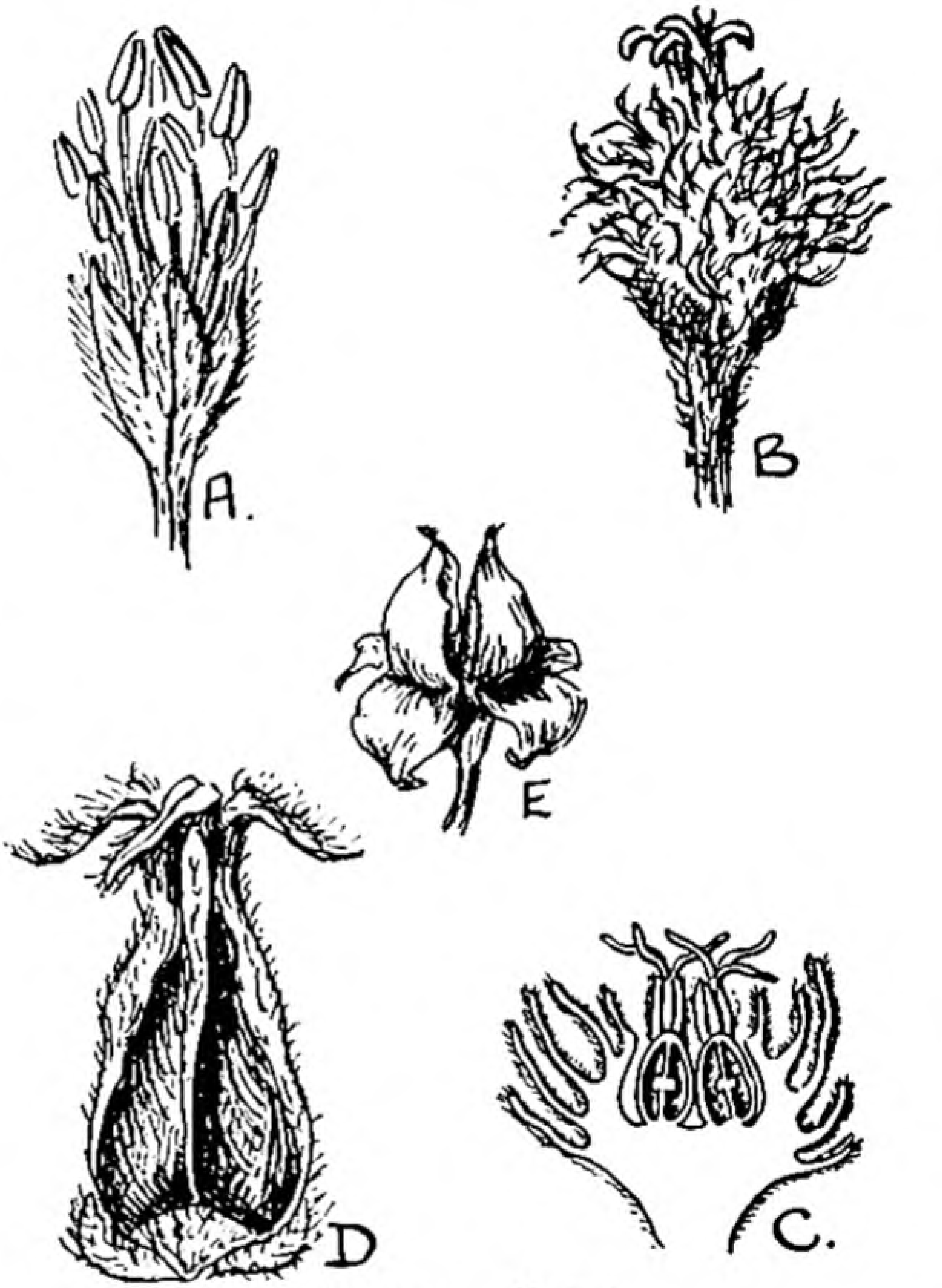

Fig. 243. *Fagus.*

A, Male flower; B, Female inflorescence; E, Fruiting stage, showing two fruits and cupule; D, Female flower, dissected out; C, Vertical section of same.

B. ORDER URTICALES. — Flowers cyclic, homoiochlamydeous, seemingly, rarely truly haplochlamydeous, rarely naked, usually 2 + 2-, rarely 2 + 3-merous, usually actinomorphic. Stamens opposite the perianth leaves. Carpels 2, syncarpous, or 1. Ovary superior, 1 ovule. Fruit a drupe or nut. Flowers usually in cymose inflorescences.

1. FAMILY **Moraceae.**—Flowers homoiochlamydeous, with persistent perianth often becoming succulent, or naked, unisexual. P2 + 2 (rarely 2–6), A2 + 2 opposite the perianth leaves, rarely

only 1. $G(\underline{2})$. Stigmas 2 or 1. Ovary unilocular. Ovule 1, pendulous, rarely basal and orthotropous. Fruit an achene or drupe. Endosperm present or absent. Embryo usually curved (Figs. 244 and 245).

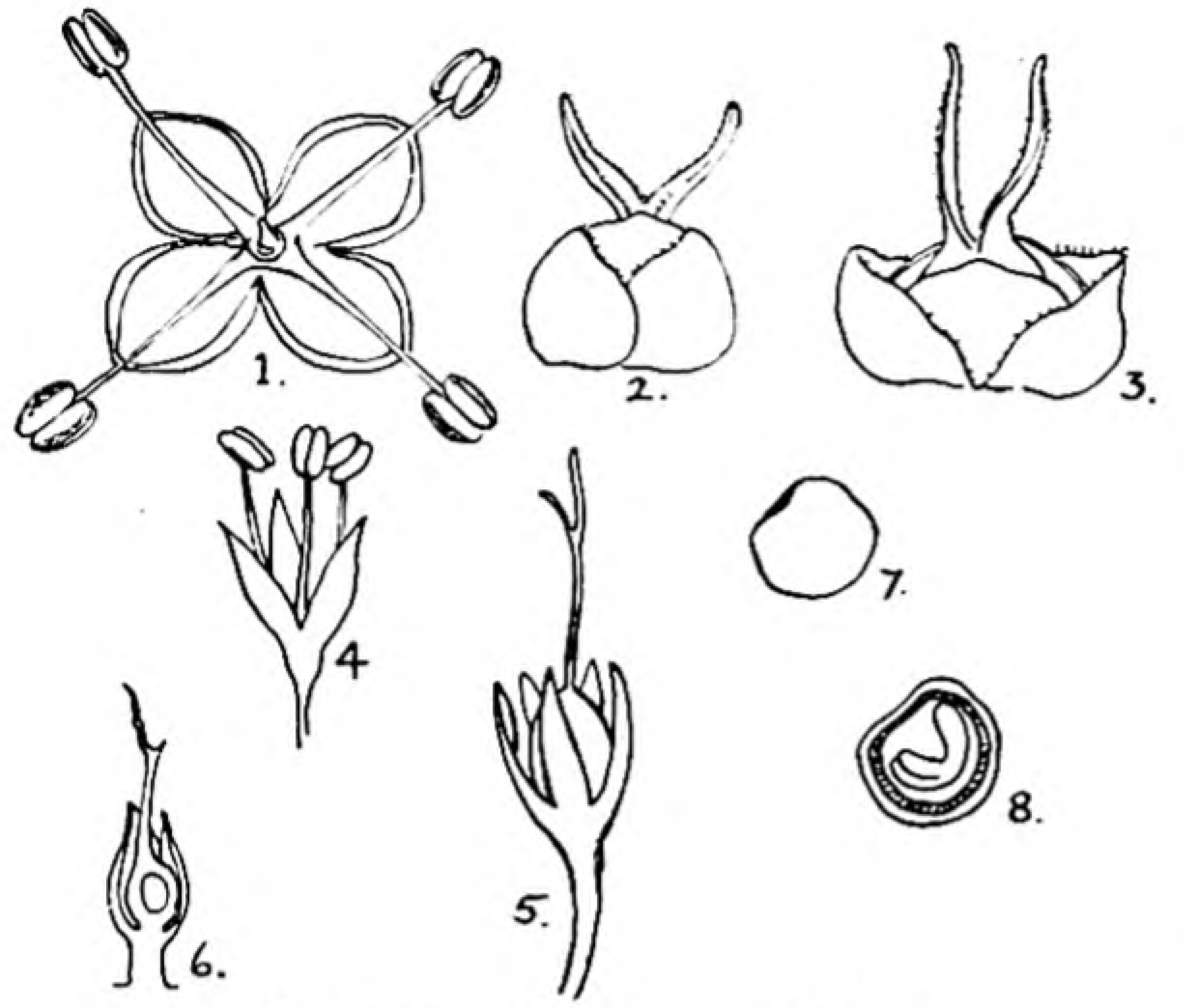

Fig. 244. *Morus* AND *Ficus*.

1. 2 & 3, *Morus;* Male and female flowers. 4-8, *Ficus;* 4, Male flower; 5, Female flower; 6, Same cut longitudinally; 7, Fruit; 8, Same in L.S.

Trees and shrubs, rarely herbs. Leaves stipulate. Flowers small, usually in cymose inflorescences which are often condensed into heads or become disc- or beaker-shaped in consequence of intercalary growth of the axis. Latex cells are present (except in *Cannabis*) and cystoliths occur (p. 26, Fig. 13).

This is a large family of about 950 species, mostly tropical and well represented in India. The genus *Ficus* contains about 700 species, mostly tropical, many of which are familiar in India. *F. bengalensis*, the banyan, extends its canopy and produces aerial roots which reach the ground and act as supports as well as absorptive organs. A famous example in the Calcutta Botanic Garden covers several acres of ground and possesses hundreds of these aerial roots. *F. elastica* is the rubber tree, cultivated in Assam. It usually starts as an epiphyte but soon sends aerial roots down to the soil and these produce strong buttress roots at their bases. Other species start as epiphytes and their roots ultimately strangle the host.

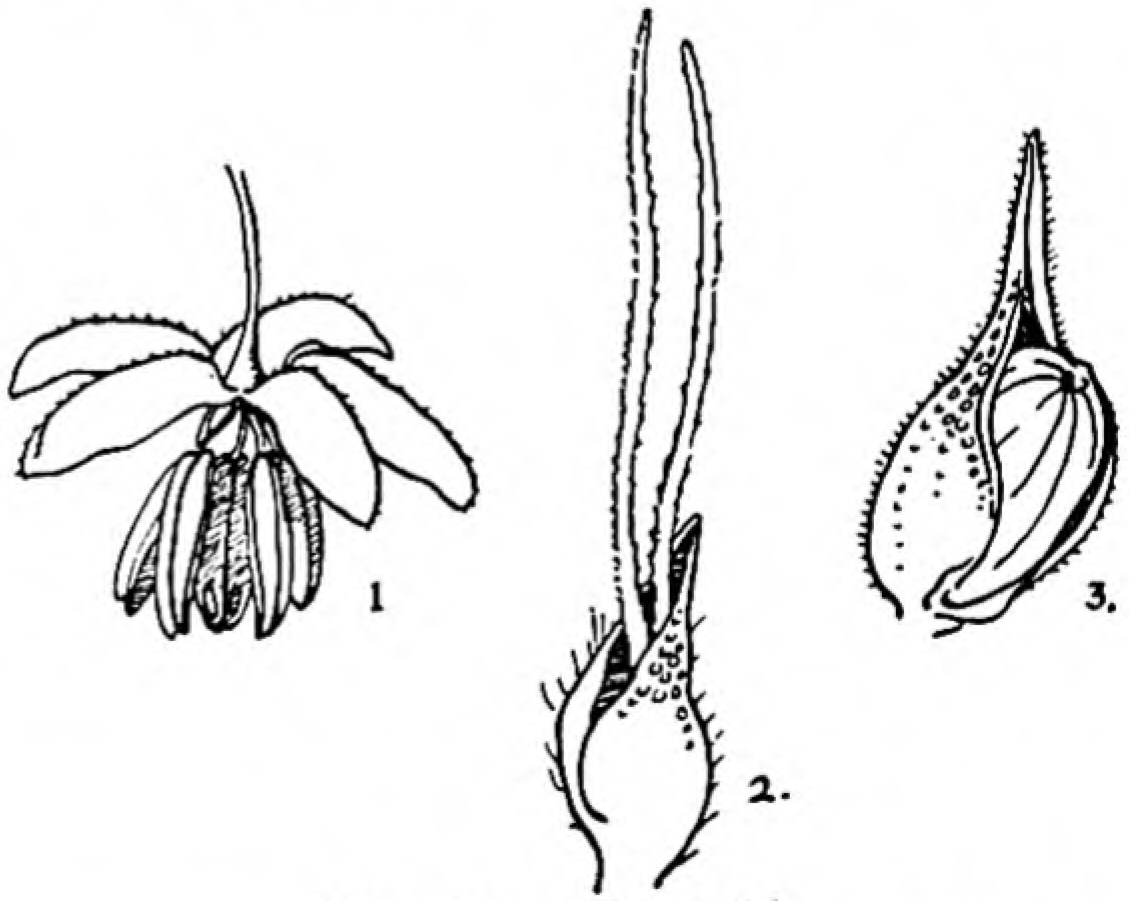

Fig. 245. *Cannabis*.

1, Male flower; 2, Female flower within its bract; 3, Fruit.

F. religiosa, the pipul, as also *F. laccifera* and other species are used as hosts for the lac insect, the source of shellac. *F. Carica* is the fig tree (anjír) and yields the edible fig (Fig. 221, A). *F. glomerata* is gúlar. *Morus alba*, var. *indica* is the Indian mulberry, grown for its fruit (Fig. 221, B) and to feed silk-worms. *Artocarpus integrifolia* yields jak fruit. *A. incisa*, bread fruit, introduced into Indo-Malaya from the Pacific is now common on the coasts. *Dorstenia indica* has an open cup-like receptacle and occurs in central and southern India. *Cannabis sativa* is the hemp, largely grown in India for its narcotic resin secreted by innumerable glandular hairs (Fig. 29, G) on the bracts of the female inflorescences and on the leaves. The consolidated flowering tops of the pistillate plants form ganja; the resin only, charras; the leaves, bhang. An intoxicating liquor, hashish, is also prepared from it. It is also cultivated for its fibre (hemp) and its " seed " which contains a valuable oil.

Broussonetia papyrifera and *B. Kaempferi* have bark which is used in paper-making (Japanese paper). *Humulus lupulus*, a north temperate plant, is the source of hops (p. 280, Fig. 221, C).

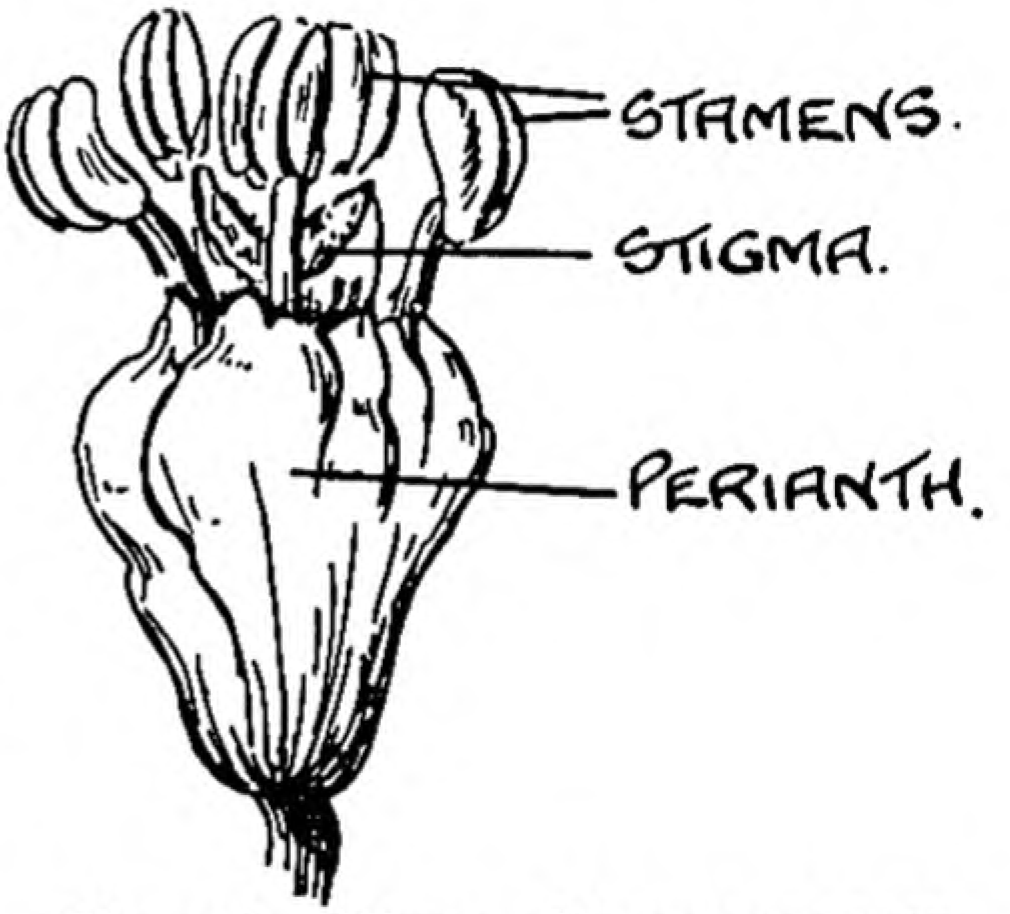

Fig. 246. *Ulmus*. HERMAPHRODITE FLOWER.

The family Moraceae (Engler, 1936) includes the sub-families Moroideae, Artocarpoideae, Conocephaloideae and Cannaboideae.

The family Ulmaceae has two sub-families, the Ulmoideae, represented by *Ulmus*, the elm, in the north temperate zone and the mountains of tropical Asia; and the Celtoideae in which *Celtis* is an important genus, found in temperate to tropical regions. *Celtis australis*, the nettle-tree, has edible fruits (drupes), and provides a useful wood and fodder. The elm supplies a valuable timber. The flowers occur in clustered dichasial cymes in the axils of the leaves of the previous year. The flowers (Fig. 246) are hermaphrodite, P(4–6) A4–6 G$(\underline{2})$. Only one loculus and one ovule develop. The fruit is a samara (Fig. 214, B) and the seed non-endospermous.

2. FAMILY **Urticaceae.**—Flowers rarely hermaphrodite, usually unisexual. Perianth 4-5 (rarely 2-3). Stamens as many, opposite the perianth leaves, curved inwards in the bud, later springing back and exploding. Always 1 stigma. Ovary unilocular with

one basal, erect ovule. Fruit an achene or drupe. Seed endospermous. Embryo straight.

This family consists chiefly of herbs, and is well represented in tropical and warm temperate climates.

The leaves are opposite (*Urtica*) or alternate and stipulate (*Parietaria*). Cystoliths are found in many of them, including *Parietaria* and species of *Urtica*. The order may be divided into two groups according as stinging hairs are present or absent. To the former group belong *Urtica* (Fig. 29, H and p. 55), *Laportea* (fever or devil nettle) and *Girardinia heterophylla* (the Nilgiri nettle); to the latter, *Parietaria*.

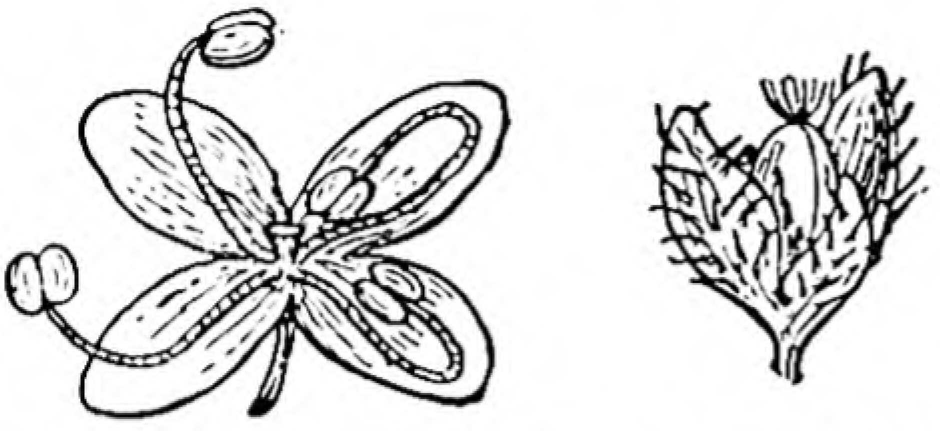

Fig. 247. Male and Female Flowers of *Urtica*.

The **inflorescences** are usually axillary cymes which may be panicled in appearance or more or less clustered. The **flowers** (Figs. 247 and 248) are regular, monochlamydeous, unisexual or, occasionally, hermaphrodite. *U. urens* and *U. pilulifera* are monoecious, the male and female flowers in the latter being borne in different panicles; *U. dioica* is dioecious; *Parietaria* is polygamous.

Perianth of four or five leaves, poly- or gamo-phyllous (four and gamophyllous in British species), green, inferior, persistent. **Stamens** equal to the perianth segments and opposite to them. The stamens are at first folded inwards and downwards in the flower, but when ripe, or when moved, they spring up violently and give out a little cloud of pollen. **Pistil** monocarpellary; ovary superior, unilocular, with one basal, orthotropous ovule. Stigma tufted and often sessile. Pollination by wind. The male flowers have a rudimentary pistil. The **fruit** is an achene enclosed in the persistent perianth. **Seed** endospermous.

Species of *Pilea* ("artillery plant") have explosive stamens. Species of *Urtica, Laportea, Debregasia, Maoutia* and *Boehmeria* are sources of fibre. *B. nivea* and *B. viridis* yield a bark-fibre of great length and strength (rhea, ramie or China grass).

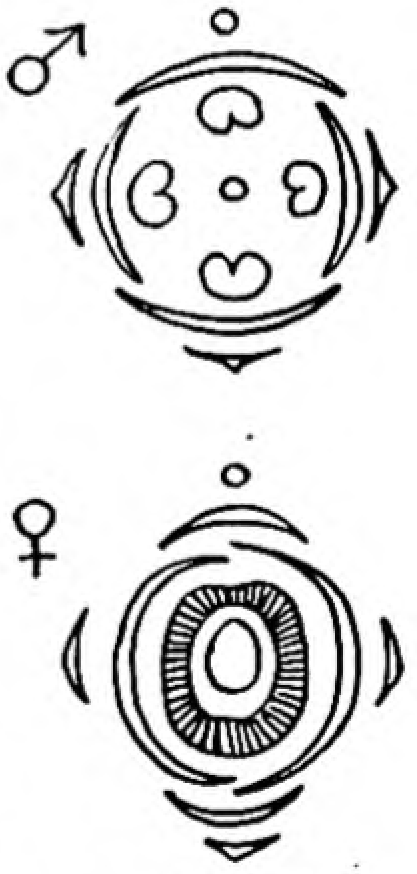

Fig. 248. *Urtica*, Floral Diagrams.

C. Order POLYGONALES.—Flowers haplo- to heterochlamydeous, actinomorphic, ovary superior, unilocular, with one basal, erect (rarely anatropous) ovule. Leaves usually have ochreate stipules.

FAMILY **Polygonaceae.**—Flowers cyclic or partially spiral, haplochlamydeous to heterochlamydeous, hermaphrodite or unisexual, actinomorphic. P3-6, A6-9, rarely fewer or more, partially doubled. G(3) or (2), rarely (4), with 3, 2 or 4 stigmas. Achenes. Seeds with copious mealy endosperm.

This family is represented in the Indian Flora by the genera *Rumex* (docks and sorrels), *Polygonum*, *Rheum* (*Rh. Rhaponticum* and *Rh. officinale* yield medicinal English rhubarb, and the succulent petioles of the former are eaten as a vegetable ; *Rh. palmatum* is the source of so-called Turkey rhubarb, cultivated in China and Tibet) and *Fagopyrum*, the buck-wheat. They are mostly herbs. The leaves are simple and alternate, with ochreate stipules, and the stems are swollen at the nodes. The acid properties found in most of the plants are due to the presence of various oxalates (p. 25).

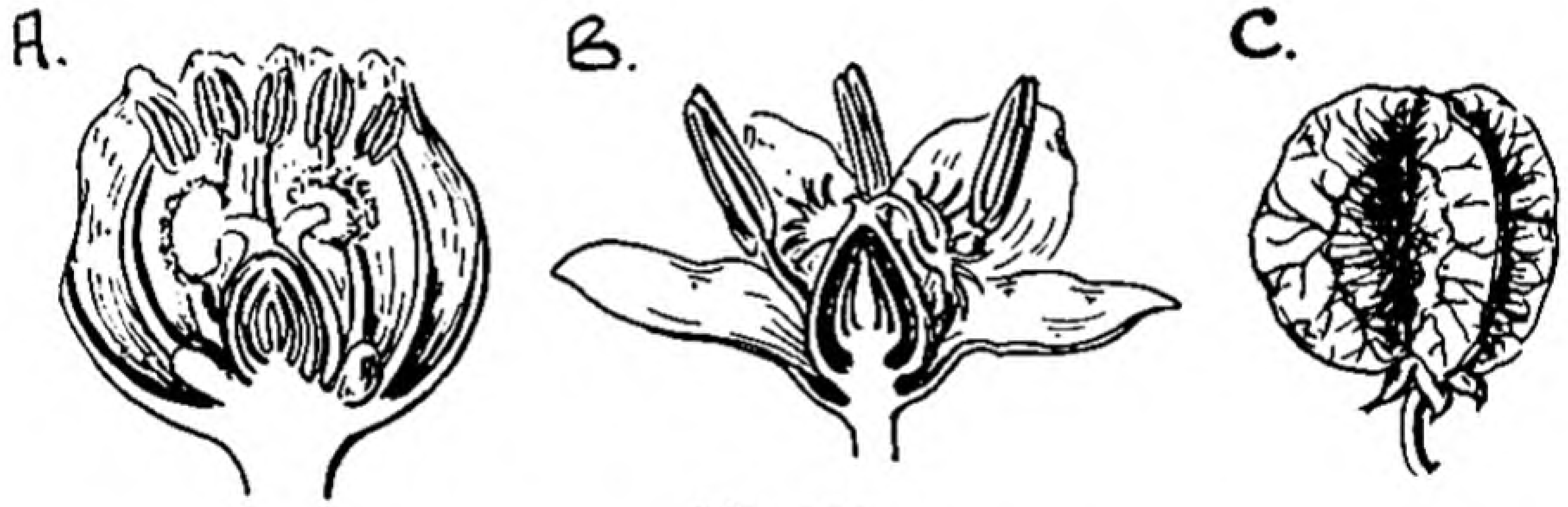

Fig. 249.

A, *Rheum officinale*, flower in vertical section; B, *Rumex acetosa*, flower in vertical section; C, *Rumex acetosa*, fruit with persistent inner perianth.

The **inflorescence** in most cases is mixed, commonly a raceme or panicle of cymes. The **flowers** are hypogynous and usually hermaphrodite. They are typically trimerous, sometimes dimerous, but the number of parts is often increased by duplication or diminished by suppression. Unisexual flowers occur in the sorrels; *Rumex acetosa*, the sorrel, is monoecious; *R. acetosella*, the sheep's sorrel, is dioecious.

The **perianth** typically consists of three sepals and three petals resembling each other, and either sepaloid or petaloid (Figs. 249 and 250). It is polyphyllous, imbricate in aestivation, inferior and persistent. This typical condition is found in *Rumex* and *Rheum*, and in these genera the *inner* segments (petals) enlarge during the development of the fruit and invest it (Fig. 249, C). In *Polygonum* (Fig. 250, C and D) the anterior segment of the inner series (petals) is suppressed so that the perianth consists of five leaves ($P3 + 2$ or $K3$ $C2$); here the three *outer* segments become enlarged and invest the fruit. In *Oxyria* there are two sepals and two petals ($P2 + 2$ or $K2\ C2$).

The **Androecium** consists fundamentally of six stamens ($A3 + 3$), but this condition is seldom found. Usually there is chorisis (= duplication or doubling) of one or more of the stamens of the outer series, and this may be accompanied by suppression of one or more members of the inner series (see Fig. 250). In *Rheum* there are nine stamens, all the outer stamens being duplicated ($A3 \times 2 + 3$). In *Rumex* the outer are all duplicated, but the inner suppressed ($A3 \times 2 + 0$). In *Polygonum* there are five to eight stamens; usually two outer stamens are duplicated, and one or more of the inner ones suppressed. In *Oxyria*, where the arrangement is dimerous, there are six stamens, the two outer duplicated ($A2 \times 2 + 2$).

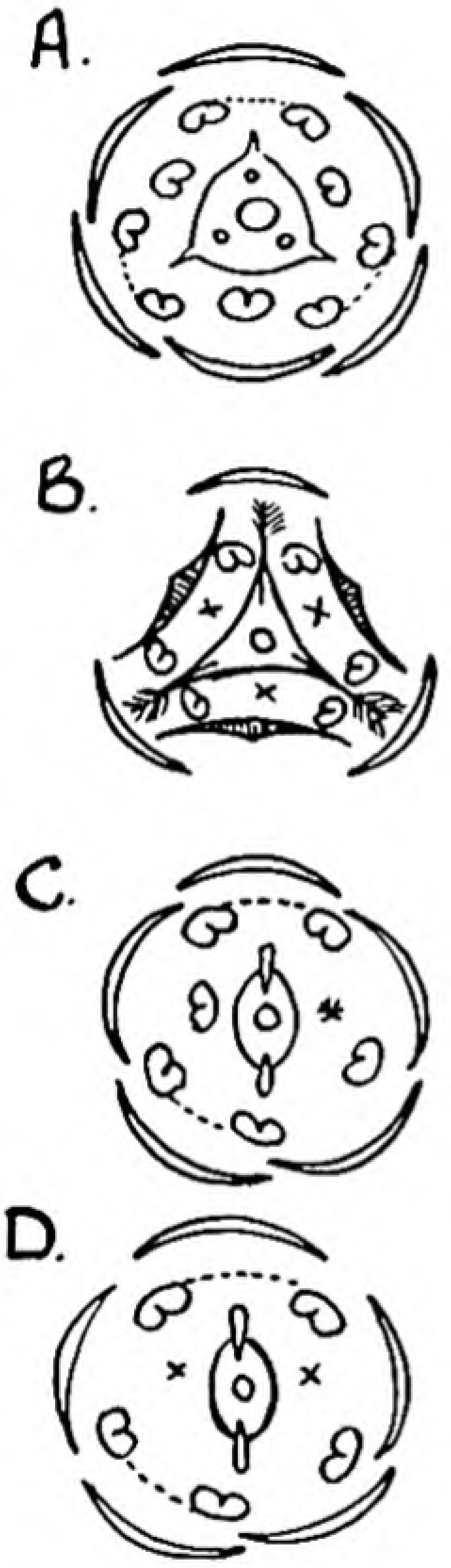

Fig. 250. Floral Diagrams.

A, *Rheum*; B, *Rumex*; C, *Polygonum lapathifolium*; D, *Polygonum amphibinium.*

The **Gynaeceum** is usually tri-carpellary and syncarpous; in *Oxyria* and some species of *Polygonum* (e.g. *P. amphibium*) it is bicarpellary (Fig. 250, C, D). The *ovary* is unilocular, superior, with one basal orthotropous ovule (Fig. 189, p. 248); *stigmas* two or three. The **fruit** (Fig. 249, C) is ovoid when there are two carpels, triangular when there are three. The persistent membranous perianth provides for wind dispersal. The **seed** is endospermous.

An annular nectar disc is present in *Polygonum* at the base of the stamens, and the flowers are entomophilous. Some species are marsh or water plants. In *P. convolvulus*, the black bindweed, the stem is twining. *P. aviculare*, the knotgrass, has cleistogamous flowers. *P. tinctorium* yields Chinese indigo.

In *Rumex* there is no nectar disc. The stigmas are long and feathery, and the flowers are wind-pollinated. *Rheum* is entomophilous. *Fagopyrum* resembles *Polygonum*, and is sometimes placed in that genus (*Polygonum Fagopyrum*).

D. Order CENTROSPERMAE.—Flowers spiral or cyclic, homoio- or heterochlamydeous. Stamens often as many as the perianth leaves and opposite them, but also numerous to one. Ovary usually superior, carpels numerous to one, usually unilocular, ovules numerous to one, campylotropous, perisperm only, curved embryo. Mostly herbs.

1. FAMILY **Chenopodiaceae.**—Flowers spiral, homoiochlamydeous, hermaphrodite or unisexual, usually actinomorphic. Perianth leaves 5, 3, 2 (rarely 4, 1, 0), imbricate. A = P or fewer, curved inwards in bud. G(2), rarely (3-5) with usually as many stigmas. Ovary superior, unilocular, one basal ovule. Fruit, achene or pyxidium, enclosed in persistent perianth.

The plants belonging to this family are widely distributed in maritime regions, many of them (halophytes) growing in salt marshes or on muddy foreshores, and showing marked xerophytic characters (see p. 166). It is represented in India by the glasswort or marsh samphire (*Salicornia*), the saltwort (*Salsola Kali*), the seablite (*Suaeda maritima*) and various species of goosefoot (*Chenopodium*) and others. *Chenopodium* is not so markedly halophytic as the other genera, various species (e.g. *C. album*) being commonly met with on waste or cultivated ground and possessing the ordinary herbaceous characters.

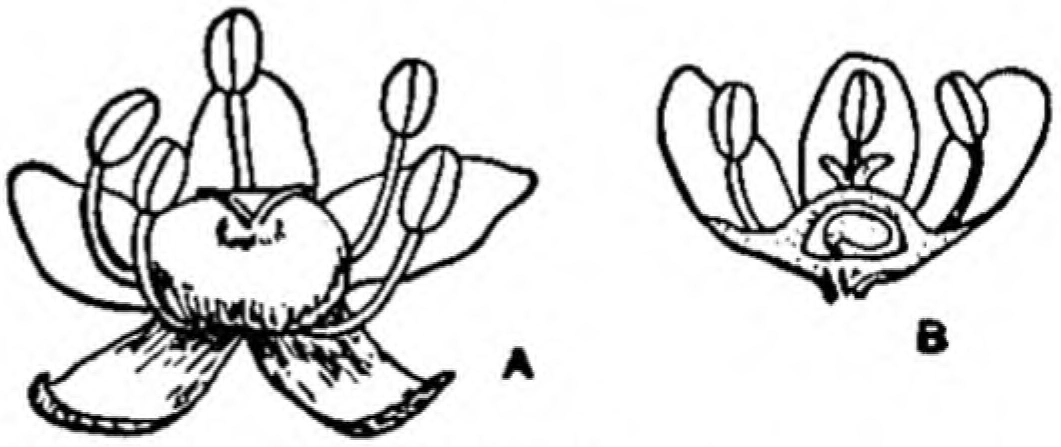

Fig. 251.
A, Flower of *Chenopodium*; B, Flower of *Beta* in longitudinal section.

The plants are mostly herbs, in which the stem and leaves are often succulent and fleshy and serve for the storage of water. The leaves are occasionally absent (e.g. *Salicornia*); when present they are exstipulate and alternate, or occasionally opposite (sp. of *Atriplex*). They often feel granular or mealy to the touch owing to the presence of small hairs; this is very noticeable in species of *Chenopodium* and *Atriplex*.

The **inflorescence** is frequently mixed; racemes, panicles, and spikes of small cymes are common. The **flowers** (Fig. 251) are small and inconspicuous, regular, monochlamydeous, hypogynous, hermaphrodite, or occasionally (*Atriplex*) unisexual and either monoecious or dioecious. They are nectarless, and either anemophilous or self-pollinated.

Perianth poly- or gamo-phyllous, small, sepaloid, and persistent. It usually consists of five leaves (the rule in *Chenopodium*, *Beta*, *Salsola*, and *Suaeda*), sometimes of three or four (*Salicornia*); in the female flowers of *Atriplex* there are only two. **Stamens** usually as many as the leaves of the perianth and opposite them, hypogynous, sometimes perigynous (*Beta*); *Salicornia* has either one or two. **Gynaeceum** of two, sometimes three, carpels, syncarpous; ovary unilocular, superior (half inferior in *Beta*) with one basal campylotropous ovule. **Fruit** a small nut enclosed in the persistent perianth. **Seed** with or without perisperm; the embryo is curved or spirally twisted round the perisperm when present.

Salicornia, the samphire, is a small leafless plant which is widely distributed and grows on muddy shores. It has succulent jointed stems. The flowers are placed two or three together in little cavities, two of which are found opposite to each other at each node. The flower has a fleshy perianth with three or four teeth, one or two stamens, and a pistil of two carpels.

There are some familiar cultivated forms. The garden beet, the sugar beet, and the mangold wurzel are cultivated varieties of the wild beet. They are biennials and sugar is stored in their roots. *Spinacia oleracea* is the true spinach; the flowers are in dichasia and are dioecious.

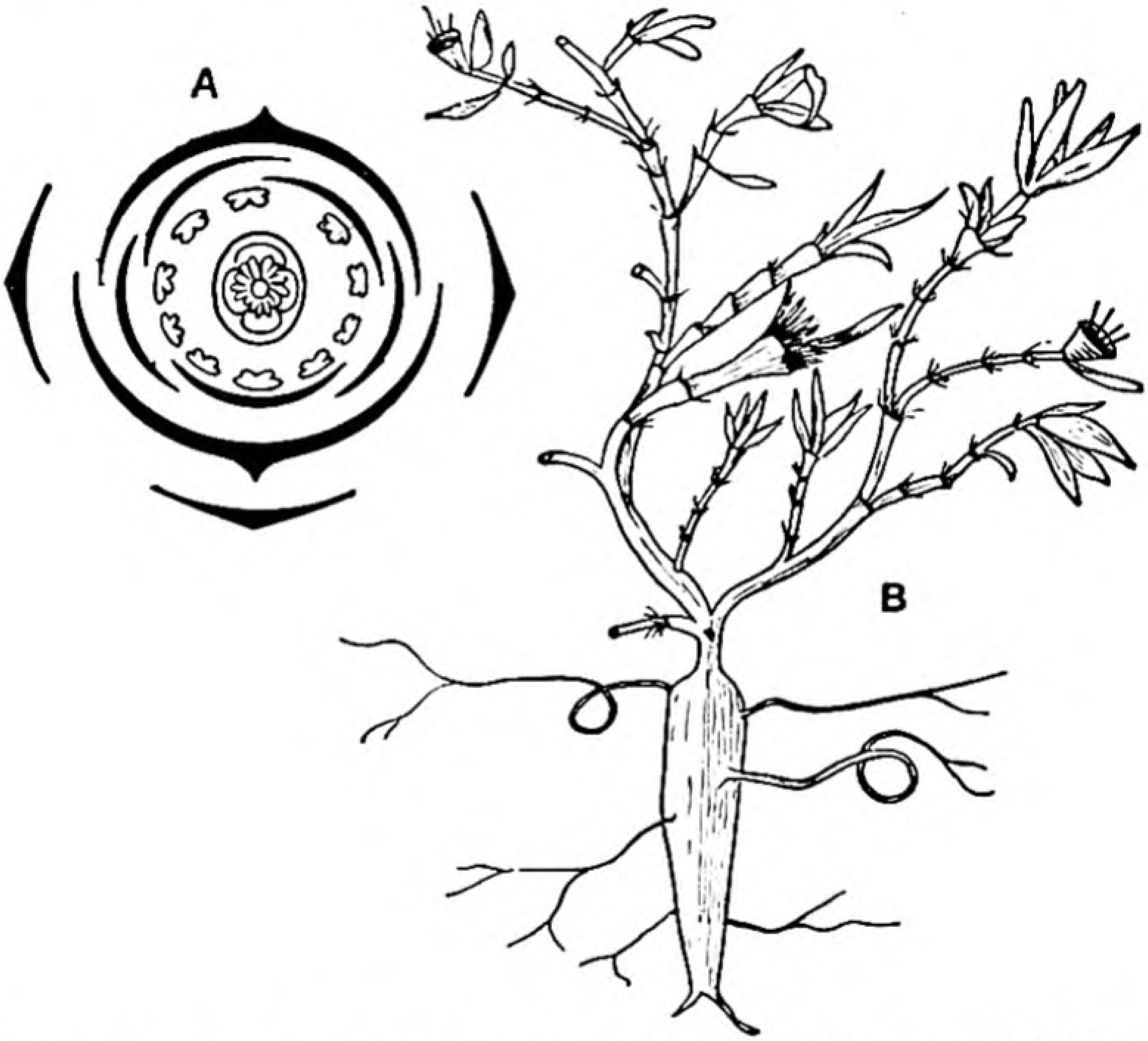

Fig. 252. A, FLORAL DIAGRAM OF *Portulaca oleracea* (AFTER ENGLER). B, PLANT OF *Portulaca tuberosa*.

2. FAMILY **Portulacaceae.**—Flowers cyclic, homoiochlamydeous, hermaphrodite, actinomorphic. P4–5 A4–5 opposite the petals, or fewer, or 5 + 5, or ∞ by splitting, G(2–8). Ovary superior or rarely semi-inferior, ultimately unilocular, with 1–∞ campylotropous ovules on a basal placenta. Fruit a capsule.

This family is well represented in India by the various species of *Portulaca* (Fig. 252), which are common on waste ground and in sunny places. They are all small herbaceous plants, growing only an inch or two high, with many sprawling lateral branches. They are usually annuals, coming up afresh every year from the seeds of the previous year, but some have tuberous storage roots. The **leaves** are small, and are generally more or less fleshy from the development of water-storing parenchymatous tissue; the plants grow in places which are liable to become very dry, and without storage of water they might succumb to desiccation during drought. The leaves are sometimes alternate, sometimes opposite, and usually possess stipules, though in some of the species these are represented by an axillary bundle of fine white hairs.

The **inflorescences** are simple; in many species the flowers are solitary, but in the others the inflorescence is of cymose nature.

The **flowers** are hermaphrodite and regular and usually hypogynous; they are usually regarded as monochlamydeous. There are two bracts, sometimes called sepals, an anterior overlapping a posterior, and usually united below; the perianth leaves are 4 or 5, distinct, and in *Portulaca*, the only common genus of the family in India, they are markedly perigynous, the ovary being adherent to the base of the sepals. The **stamens** are 4 or 5, or sometimes twice or three times as many, but in *Portulaca* they are 4 to ∞; the **ovary** is usually superior, but in *Portulaca* is half-inferior, of (2–8) usually (3) carpels, and is unilocular with a basal placenta which bears numerous ovules, while the number of carpels is indicated by the number of stigmas.

The flowers secrete nectar and are visited by flies and other insects. They close at night and in dull weather. On withering the stamens and style crumple up together, and self-fertilisation occurs. The stamens of *Portulaca oleracea* are slightly sensitive to contact, and move towards the side touched.

The only Indian genus is *Portulaca* itself, though there are sometimes others to be seen in ornamental gardens. The genus *Portulaca* is abnormal in possessing a semi-inferior ovary. Among the common species are *P. oleracea*, the purslane, which is a common pot-herb in many parts of the world, and has alternate flattish exstipulate leaves, rather closely crowded together, and bunches of flowers; *P. quadrifida*, with opposite flat leaves, stipules composed of bunches of hairs, and single flowers; *P. tuberosa* (Fig. 252, B), on rocks on the seashore, with nearly cylindrical fleshy leaves and single flowers. Many varieties of *Portulaca* are cultivated.

3. Family **Caryophyllaceae.**—Flowers cyclic, haplo- or heterochlamydeous, 5-(4-) merous, diplostemonous, rarely haplostemonous, usually hermaphrodite, actinomorphic. G(5-2). Ovary superior or semi-inferior, usually unilocular, ovules one to numerous on a basal free-central placenta. Fruit a capsule or berry. Seeds with perisperm; embryo curved round it.

The plants belonging to this family are mostly herbs of temperate regions, with swollen nodes and opposite, simple, entire, and usually exstipulate leaves, e.g. pink, sweet william, chickweed, and various species of campion. The **inflorescence** is cymose, typically a dichasium (Fig. 202). The **flowers** are regular, usually hermaphrodite and pentamerous, exceptionally unisexual or tetramerous.

Calyx polysepalous or gamosepalous, of 5 (or 4) sepals. **Corolla** polypetalous, of 5 (or 4) petals; occasionally the petals are wanting. **Androecium** of 10 (or 8) free stamens (in some species reduced to 5, 4, or 3), hypogynous (or occasionally perigynous), obdiplostemonous. **Gynaeceum** of 2-5 carpels, syncarpous, with free styles (Fig. 185, C); ovary unilocular, superior; ovules usually numerous, amphitropous or campylotropous, with free central placentation (see p. 248). **Seed** with embryo curved round the perisperm. **Fruit** usually a unilocular capsule dehiscing by teeth separating at the apex (Fig. 222, B); seeds scattered by the censer mechanism (p. 281).

In the Caryophyllaceae there are two very distinct types of flower structure, and corresponding to this the family is subdivided into two groups or tribes:—

I. The **Alsinoideae,** the simpler type, in which the sepals are free or only slightly united at the base, and the petals are short. The flowers are shallow and wide open therefore, and the nectar, which is secreted by glands at the bases of the stamens, is accessible to a variety of short-tongued insects (flies, etc.). The flowers are usually protandrous, but some are homogamous and self-pollinated. In this group the leaves are sometimes stipulate, the flowers may be more or less perigynous, and there is frequently reduction in the number of petals or stamens.

II. The **Silenoideae,** in which the calyx is gamosepalous and tubular, and the petals are long and clawed (Fig. 174, A). The flowers are therefore closed up, and the nectar, which is secreted by the receptacle between the calyx and corolla, can be reached only by long-tongued insects (bees, butterflies, and moths). Small insects are further excluded in some species by the presence of ligules on the petals. The flowers are usually distinctly protandrous.

I. **Alsinoideae.**—*Stellaria,* $K5\ C5\ A5 + 5\ G\underline{(3)}$, petals deeply 2-lobed appearing like 10, rarely absent, flowers more or less perigynous. Many species common in the hills, but a few descend to the plains, preferring moist shady places. *Cerastium vulgatum,* mouse-ear chickweed, a very variable plant, is found in the hills all over India.

II. **Silenoideae.**—Floral formula $K(5)\ C5\ A5 + 5\ G\underline{(2-5)}$. In the genus *Lychnis* there are 5 carpels. Species of *Lychnis* occur in the hills.

The genus *Silene* is distinguished from *Lychnis* by its three styles. *S. conoides* descends to the Punjab plains.

The genus *Dianthus,* species of which occur in the hills, includes the cultivated pinks, carnations, picotees, and sweet william. There are two carpels. The flowers are adapted for pollination by butterflies.

The Caryophyllaceae are classified near the Chenopodiaceae, because in both families the embryo is curved round the perisperm in a characteristic manner.

E. ORDER RANALES.—Flowers spiral, spirocyclic or cyclic, rarely achlamydeous, haplochlamydeous to usually heterochlamydeous, hypogynous to epigynous, actino- or zygo-morphic, stamens usually ∞. Carpels ∞–1, usually free, rarely fused.

1. FAMILY **Ranunculaceae.**—Flowers cyclic, spirocyclic, rarely completely cyclic, haplochlamydeous to heterochlamydeous, in the former case with petaloid perianth, often with nectaries between this and the stamens, usually hermaphrodite, actinomorphic, rarely zygomorphic. Stamens numerous, free. Carpels numerous to 1, rarely syncarpous, with numerous to 1 ovule, with 1-2 integuments. Fruits usually achenes or follicles, rarely a berry. Endosperm copious, oily, with small embryo.

The **inflorescence** is in most cases cymose, e.g. *Ranunculus*. In *Aconitum* and *Delphinium* racemes are found. In *Anemone* the flowering shoot bears a terminal flower.

The flowers are hermaphrodite, mostly actinomorphic; in *Aconitum* and *Delphinium* they are zygomorphic.

The **perianth** seldom shows distinct calyx and corolla. This does occur, however, in the largest genus *Ranunculus*, where there are typically five sepals and five petals (Fig. 172). In many cases between the outer perianth leaves and the stamens there are nectaries of various forms. These have commonly been regarded as *modified petals*. According to this view the outer perianth leaves represent a petaloid calyx. The term calyx is also applied to a single series of perianth leaves, when there are no nectaries, on the ground that in such a case the petals have disappeared altogether. It is convenient to adopt this view in describing the various types, although it is possible that the nectaries have been derived from the outer stamens. It should be noticed that nectaries in some genera are developed in connexion with the sepals, stamens, or carpels.

The **stamens** are indefinite in number (∞), hypogynous, free; anthers innate, extrorse. The **gynaeceum** is usually polycarpellary, apocarpous; the number of carpels varies. There may be one or a number of anatropous ovules in each ovary; if one, it may be erect or pendulous.

The **seed** is endospermous. The **fruit** may be an etaerio of achenes, or of follicles—rarely a berry, or (owing to exceptional fusion of the carpels) a capsule.

Pollination.—The flowers are usually protandrous, but those of *Thalictrum* and *Helleborus* are protogynous, and those of *Anemone* and *Trollius* are homogamous. *Ranunculus*, in which the nectar is only partially concealed, is visited by various insects. The flowers of *Adonis* and *Thalictrum*, as also those of *Anemone* and *Clematis*, are "pollen-flowers"; but some species of *Thalictrum* are wind-pollinated, and in some species of *Anemone* and *Clematis* nectar is secreted by staminodes only partially concealed.

The flowers of *Trollius* and *Anemone* are often self-pollinated, and in most of the other genera self-pollination may occur, but in *Helleborus* it is precluded by the absolute protogyny of the flower. The most highly specialised flowers are those of *Aquilegia*, *Delphinium*, and *Aconitum*. They are suited for pollination by long-tongued bees (chiefly humble-bees).

Most of the Indian Ranunculaceae grow in the hills, some ascending to the alpine zone in the Himalaya, and mostly above 6000 ft. in the W. Ghats, Nilgiris, etc.

Ranunculus (Figs. 172 and 253, A-D).—This genus includes the buttercups (crowfoots) and spearworts. Typical floral formula $K5\ C5\ A\infty\ G\underline{\infty}$. Each petal has a little pocket-shaped nectary at the base. The fruit is an etaerio of achenes. *R. sceleratus*, the celery-leaved buttercup, is an annual growing in ditches, and extends to the plains from the Punjab to Bengal. There is no scale to the nectary at the base of the petal. Several other species occur, e.g. *R. reniformis*, *R. subpinnatus*, *R. Wallichianus*, and *R. muricatus*.

Clematis: actinomorphic; 4 petaloid sepals; petals 0; fruit an etaerio of achenes with persistent hairy styles. Climbing shrubs, petioles acting as tendrils. *C. Gouriana* is a common species.

Naravelia zeylanica is also a common climbing shrub whose terminal leaflets may form tendrils, and whose achenes have twisted, feathery styles.

Anemone: actinomorphic; 4–20 petaloid sepals; petals 0; fruit an etaerio of achenes. *A. rivularis* perennates by means of a root-stock sheathed in fibres.

Thalictrum (meadow rue): actinomorphic; 4 or 5 more or less petaloid sepals which fall off early; petals 0; the stamens form the attractive part of the flower; fruit an etaerio of achenes. *T. javanicum* and *T. foliolosum* occur in India.

Aquilegia (*A. vulgaris*, columbine, Fig. 253, E-H): actinomorphic; 5 petaloid sepals; 5 petaloid spurred petals, secreting nectar and hooked at the end; 5 carpels; fruit an etaerio of follicles. *A. pubiflora* occurs in India.

Aconitum (*A. Napellus*, monkshood, Fig. 176): zygomorphic; 5 petaloid sepals, the posterior one large and galeate; 2 petals represented by nectariferous organs enclosed in the hood of the calyx; carpels 2–5; fruit an etaerio of follicles. *A. heterophyllum* is the atís, whose roots are used in medicine.

Delphinium: zygomorphic; 5 petaloid sepals, the posterior one spurred; 2 spurred petals projecting into the spurred sepal and secreting nectar; carpels 1-5; fruit an etaerio of follicles (sometimes a single follicle).

2. FAMILY **Anonaceae.**—Flowers spirocyclic, usually heterochlamydeous, commonly hermaphrodite, actinomorphic. Perianth usually of 3 trimerous whorls. Stamens usually ∞, spiral. Carpels $\infty - 1$, usually free. Ovules $\infty - 1$, ventral or basal, with 2 integuments. Fruit generally a berry, seeds with ruminate endosperm and small embryo. Trees and shrubs. Leaves undivided, in two ranks, exstipulate. Oil ducts are present. In the secondary phloem rings of sclerenchyma alternate with soft bast. Tracheides with indistinct bordered pits. About 800 species, mostly tropical.

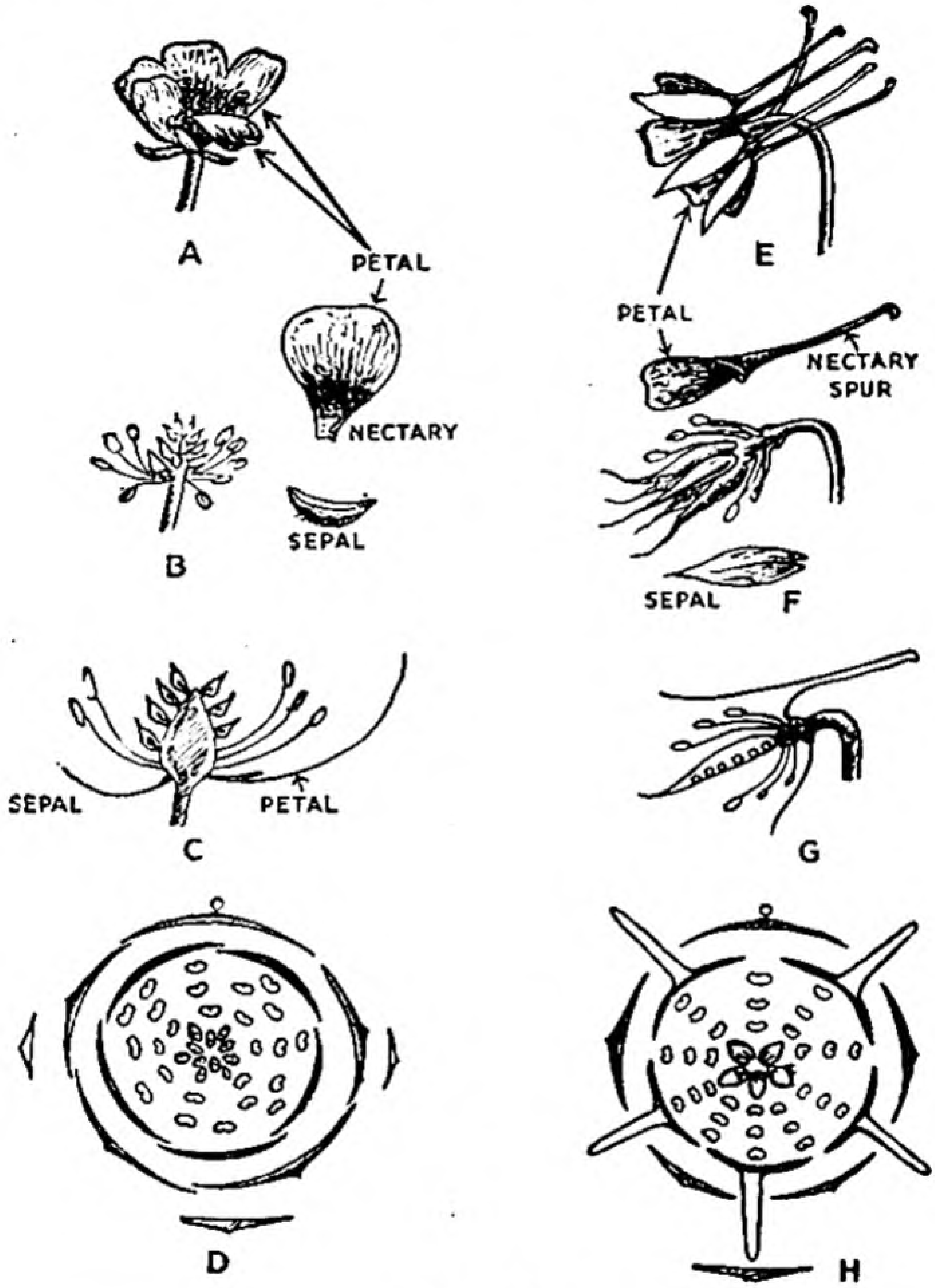

Fig. 253.

A, *Ranunculus* Flower; B, Some parts of A; note the nectary at petal-base, and the boat-shaped sepal; C, Longitudinal Vertical section; D, Floral Diagram; E-H, ditto for *Aquilegia* (Columbine).

The flowers are either solitary or in inflorescences of various kinds. The outer perianth leaves may be sepaloid, the inner petaloid. Stamens hypogynous. Ovary apocarpous (except *Monodora*). Fruit commonly an aggregate of berries which are sometimes constricted between the seeds.

In the genus *Anona* the berries, united to the receptacle, form a compound fruit which, in some cultivated species, is edible (Fig. 254, 1-3). *A. muricata* is the soursop (mamphal); *A. reticulata*, the bullock's heart or custard-apple (rámphal); *A. squamosa*, the sweetsop or sugar-apple (sharífa or sítáphal).

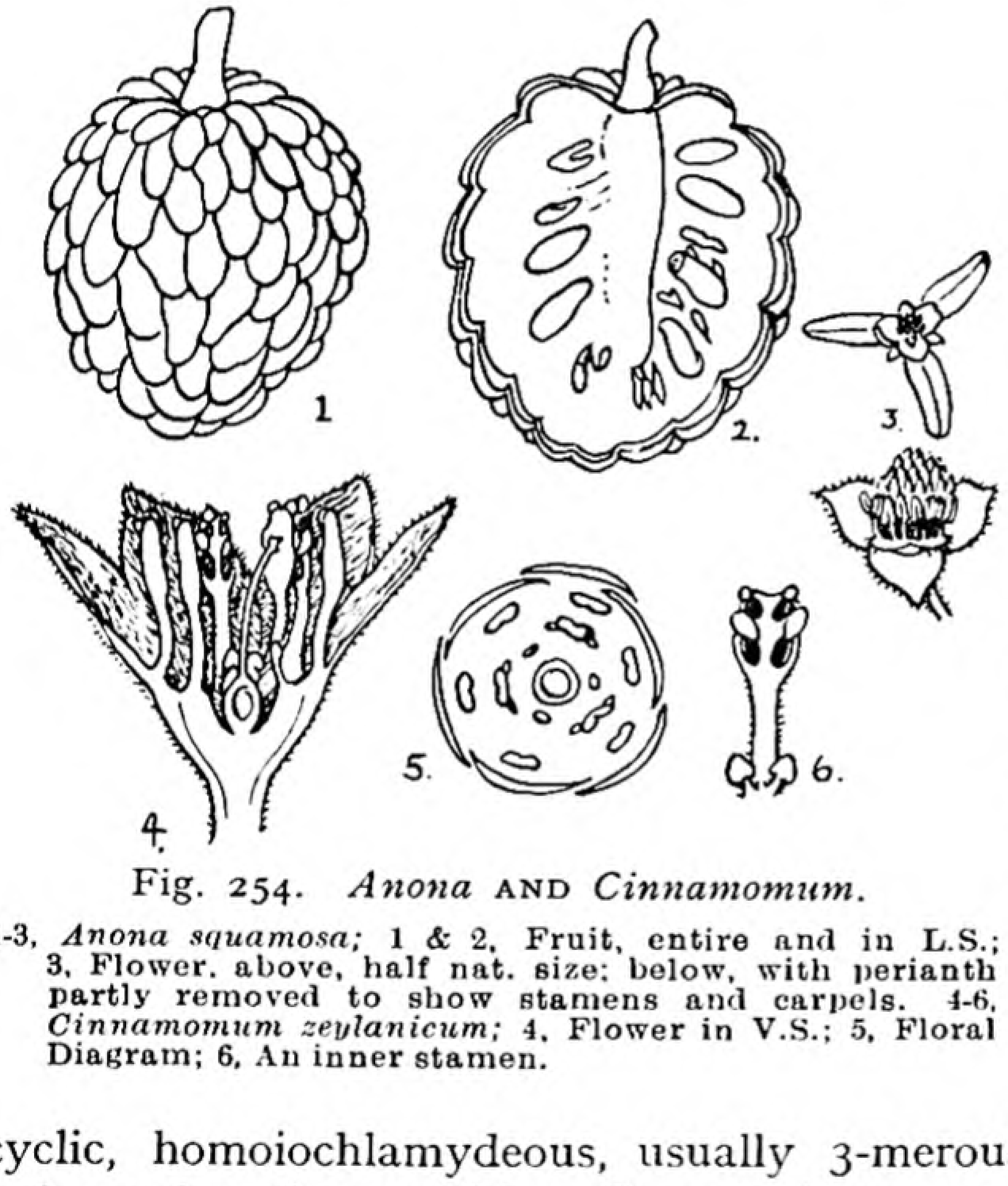

Fig. 254. *Anona* AND *Cinnamomum*.

1-3, *Anona squamosa*; 1 & 2, Fruit, entire and in L.S.; 3, Flower. above, half nat. size; below, with perianth partly removed to show stamens and carpels. 4-6, *Cinnamomum zeylanicum*; 4, Flower in V.S.; 5, Floral Diagram; 6, An inner stamen.

Cananga odorata (Indo-Malay) is cultivated for its flowers which yield macassar oil.

Artabotrys species are cultivated for their edible fruits, and sweetly scented flowers and oil. The recurved hooks by which they climb are modified inflorescence axes.

The seeds of *Monodora myristica* (tropical Africa) are sometimes used as nutmegs.

3. FAMILY **Lauraceae**.–Flowers cyclic, homoiochlamydeous, usually 3-merous, hermaphrodite or unisexual, actinomorphic. Receptacle cup- or dish-shaped. Perianth small, in two whorls, perigynous. Stamens in 3-4 whorls of which one may be staminodial; anthers opening by valves, introrse except those of the inner whorl which may be extrorse. Carpels regarded variously as 1 or 3, unilocular with one pendulous anatropous ovule with 2 integuments. Fruit fleshy and more or less enclosed in the fleshy receptacle. Seeds non-endospermous with a thin testa; embryo straight, with large cotyledons.

Trees and shrubs with usually leathery, exstipulate leaves, evergreen, alternate. Mucilage and oil cells are present in the leaves and bark.

There are over 1000 species in warm countries. The family is well represented in Indo-Malaya and contains important economic plants.

The genus *Cinnamomum* includes *C. zeylanicum* (Fig. 254, 4-6), the bark of which is stripped, scraped of its outer tissues, dried in compound quills and sold as cinnamon (dálchini); *C. Cassia*, whose bark is only partially scraped, dried in simple quills and known in commerce as Chinese cinnamon; *C. Camphora* yields camphor (káfúr), distilled from the leaves and the wood.

Persea gratissima is native to tropical America, but is widely cultivated in India. It was introduced by the Portuguese. The fruit, known as the alligator pear or avocado, is fleshy and encloses one large seed.

Cassytha is a parasite, leafless and without chlorophyll, having the general habit and behaviour of *Cuscuta* (p. 197).

F. ORDER RHOEADALES.—Flowers cyclic (not always in the androecium), heterochlamydeous, rarely apopetalous or homoiochlamydeous, hypogynous, actinomorphic or zygomorphic. Ovary superior. Carpels numerous to 2, syncarpous. Ovules with 2 integuments.

FAMILY **Cruciferae.**—Flowers cyclic, hermaphrodite, actinomorphic. K2 + 2, C4, diagonal, A2 (usually shorter) + 4 (longer), G(2). Placentation parietal, ovary usually bilocular with false-septum. Ovules anatropous or campylotropous. Fruit usually a siliqua or silicula, rarely a lomentum. Seeds non-endospermous.

The plants belonging to this family are herbaceous, occasionally shrubby. The leaves are alternate and exstipulate. There are about 3000 species, mostly temperate.

The **inflorescence** is usually a raceme or corymb; there are no bracts. The flower as a whole (Fig. 177, A) is usually isobilateral, occasionally zygomorphic. The polysepalous **calyx** consists of four sepals in two whorls. The lateral sepals are more or less saccate or pouched at the base. The **corolla** is polypetalous and cruciform. The petals are usually clawed.

The **androecium** consists of six hypogynous stamens in two whorls, and is *usually* tetradynamous; the two short *lateral* stamens form the outer whorl; the four inner stamens may be regarded as having been produced by chorisis (p. 311). The nectaries are small green glands, situated on the receptacle at the bases of the short stamens; the nectar gathers in the pouches of the lateral sepals.

The **gynaeceum** is bicarpellary and syncarpous; the ovary is superior, and bilocular, owing to the development of a false septum between the two parietal placentas (Fig. 190); the ovules usually numerous, amphitropous, or campylotropous. The **fruit** (Fig. 216) is a siliqua or silicula, rarely a lomentaceous siliqua (radish). The **seed** is non-endospermous; the testa is frequently mucilaginous (mustard, and garden cress), and thus serves to fix the seed to the soil favourably for germination. The embryo is always folded (Fig. 216).

Typical formula: $K2 + 2\ C4\ A2 + 4\ G(\underline{2})$.

Recently it has been suggested that the cruciferous ovary is really built up of four carpels. According to this view, which is supported by a weight of evidence, the two lateral carpels are sterile. Two fertile carpels lie in the antero-posterior plane. They are represented by the replum and terminate above in the two stigmas. Each fertile carpel has an inward extension. These meet and fuse in the developing ovary, and so form the "false" septum (Fig. 190).

Pollination.—The flowers are mostly homogamous, or only slightly protandrous, and self-pollination often occurs. Small flowers with spreading sepals are visited by short-tongued insects (flies, etc.), and some of them (e.g. shepherd's purse, whose flowers often have only 2-4 stamens when produced in the colder months) are regularly self-pollinated. The larger flowers, in which the sepals are erect and hold the clawed petals together so as to form a sort of flower-tube, are visited by bees and butterflies, the nectar being partially concealed and protected from rain. The large light-coloured evening-scented flowers of *Hesperis* and some stocks are visited by moths.

The arrangement in corymbs should be noticed (Fig. 196). Frequently the outer petals of the outer flowers of the corymb are larger than the inner ones so that the corollas are zygomorphic.

Not many Cruciferae occur in India. Species of *Nasturtium*, including *N. officinale*, the watercress, are found in hilly districts; also *Cardamine* species. The shepherd's purse, *Capsella Bursa-pastoris* is a weed of cultivation, especially at higher elevations. Several species are found in cultivation, or as escapes: *Sinapis (Brassica) alba* is the white mustard, a native of Europe, grown for its seed; *Brassica nigra*, the black mustard; *B. juncea*, Indian mustard (rai); *B. oleracea*, the cabbage; brussels-sprout, cauliflower and kohl-rabi; *B. Napus*, the rape; *B. rapa*, the turnip; *Lepidium sativum*, garden cress; *Raphanus sativus*, radish (múli); *Eruca sativa*, rocket (taranuri, asan); *Senebiera didyma*, lesser wart-cress.

G. ORDER ROSALES.—Flowers cyclic, rarely spirocyclic, heterochlamydeous, rarely apopetalous, hypogynous to epigynous, actinomorphic or zygomorphic, carpels free or fused, ovules few or numerous on enlarged placentae.

1. FAMILY **Rosaceae.**—Flowers cyclic, heterochlamydeous, rarely, apopetalous, usually 5-merous (rarely 3-, 4-, 6-, 8-) actinomorphic, rarely zygomorphic. Receptacle flat, bowl- or cup-shaped, often convex in the middle. Sepals, petals and stamens often perigynous or epigynous on the rim of the receptacle. Stamens usually 2-4 times as many as the sepals, or numerous, rarely only 1-5, curved inwards in the bud. Carpels as many as sepals, or 2-3 times as many, or numerous, rarely only 1-4, free or fused with the inner wall of the receptacle, unilocular, usually with 2 (rarely more or one) anatropous ovules, style terminal or arising near the base of the ovary. Fruit either an aggregate of achenes (or, more rarely, follicles) or drupes, or a single drupe, or forming a pseudocarp with the enlarged receptacle. Endosperm slight or absent.

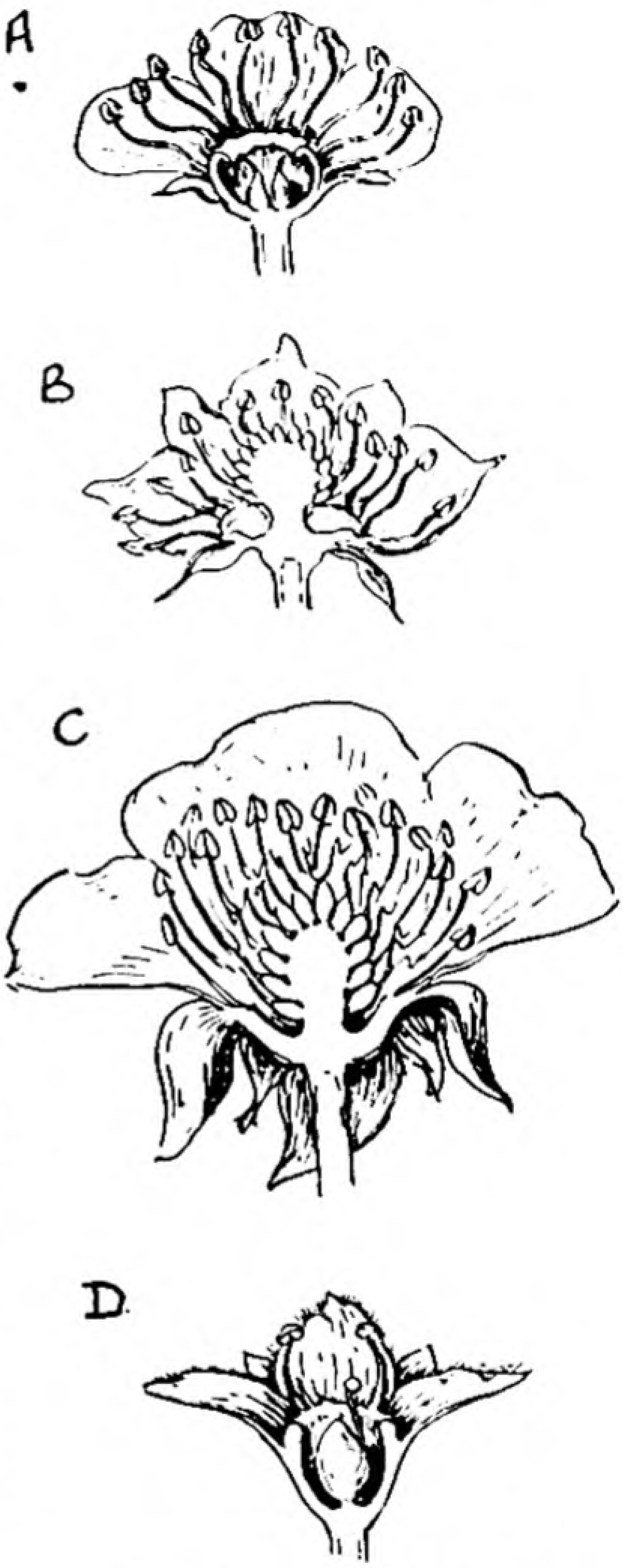

Fig. 255. FLOWERS CUT LONGITUDINALLY.

A, *Spiraea decumbens*; B, *Potentilla palustris*; C, *Geum urbanum*; D, *Alchemilla alpina*.

This is a large family of herbs, shrubs, and trees. The leaves are alternate, simple, or compound, and usually stipulate. The stipules may be leafy. Vegetative reproduction by means of runners and suckers is of common occurrence. The family is distinguished from Ranunculaceae by the shape of the receptacle, and the whorled arrangement of the floral leaves. Familiar examples are the rose, strawberry, raspberry, apple, pear and quince.

The **inflorescence** is very various, and includes both racemose and cymose forms. The **flowers** (Figs. 174, 255-257) are regular, pentamerous (or tetramerous), usually hermaphrodite, perigynous (occasionally practically epigynous, owing to fusion of the carpels with the receptacle).

The **calyx** is gamosepalous, of five (or, occasionally, four) sepals. An epicalyx is sometimes present, e.g. strawberry (Fig. 175). The **corolla** is polypetalous and rosaceous, with usually five petals, imbricate in the bud; the petals are occasionally wanting, e.g. in lady's mantle. **Stamens** two, three, or four times as many as the petals, or ∞. **Gynaeceum** of 1 to ∞ carpels, apocarpous or syncarpous. There are usually 1 to 2 anatropous ovules in each carpel. **Fruit** various—a drupe, a pome, etaerios of drupes, achenes, or follicles. The **seed** is non-endospermous.

The order gives a good illustration of the various forms of perigyny (see Figs. 174 and 255). The great variety of fruits is due to various causes—persistence or non-persistence of the receptacle, dryness or fleshiness of pericarp or receptacle, number and form of ripe carpels, etc.

Pollination.—Except in salad burnet (*Poterium sanguisorba*), which is wind-pollinated, the flowers are entomophilous, and mostly visited by all sorts of insects. *Rosa canina, Agrimonia* and *Filipendula* are pollen-flowers; but in most cases nectar is produced by the whole inner surface of the receptacle, or there is a ring-like nectary round the receptacle mouth within the insertion of the stamens.

The flowers are often more or less protogynous (e.g. apple), sometimes homogamous (e.g. cherry), or protandrous (*Rosa* sp., *Potentilla, Filipendula*, etc.). Self-pollination is apparently possible in all cases.

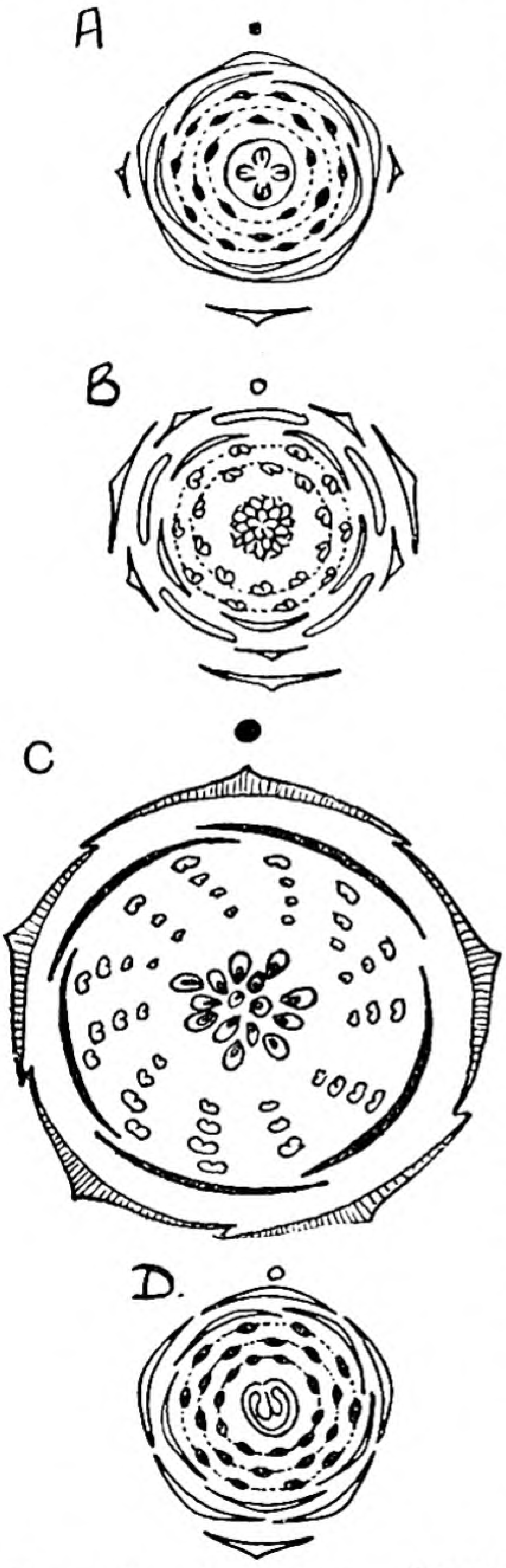

Fig. 256. ROSACEAE. FLORAL DIAGRAMS (after Engler).

A, *Pyrus communis*; B, *Potentilla palustris*; C, *Rosa*; D, *Prunus padus*.

The following are the more important sub-families:—

I. **Spiraeoideae.**—Carpels 12-1, usually 5-2, whorled, usually not sunk in the axis nor borne on a gynophore, with ∞-2 ovules, fruits dry, dehiscent, stamen filaments taper from a broad base upwards (Fig. 255, A).

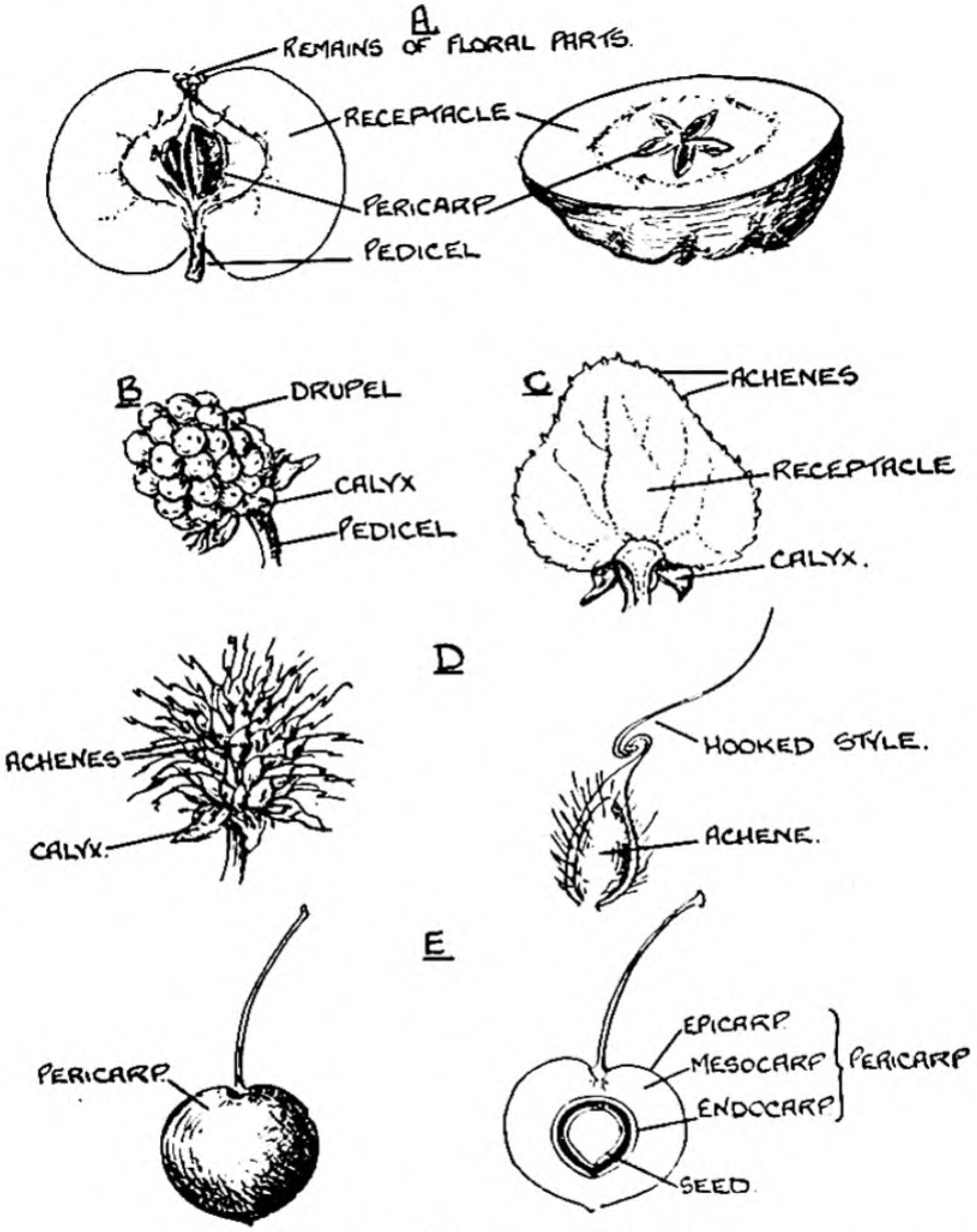
A
REMAINS OF FLORAL PARTS.
RECEPTACLE
PERICARP
PEDICEL
B
DRUPEL
CALYX
PEDICEL
C
ACHENES
RECEPTACLE
CALYX.
D
ACHENES
CALYX
HOOKED STYLE.
ACHENE.
E
PERICARP
EPICARP
MESOCARP
ENDOCARP
PERICARP
SEED

Fig. 257. FRUITS OF ROSACEAE.

A, *Pyrus*, apple in longitudinal section and transverse section; B, *Rubus*, blackberry, etaerio of drupels; C, *Fragaria*, strawberry, longitudinal section; D, *Geum*, etaerio and one achene showing hooked style; E, *Prunus*, cherry, external, and longitudinal section.

Many species of *Spiraea* are cultivated; the fruit usually consists of 5 follicles, more or less united at the base. Typical formula: $K(5)\ C5\ A5+5\ \underline{G5}$. *S. canescens* and *S. belli* occur in the temperate Himalaya. *Quillaja Saponaria* from Chile yields soap-bark.

II. **Pomoideae.**—Fruit a pome, in which the 2-5 carpels become adherent to and enclosed by the fleshy receptacle (cf. Figs. 174, F, 256, A, 257, A).

Pyrus communis (Náspátí) pear, and *P. Malus* (Seb), apple, have 5 carpels each with 2 seeds. In *Cotoneaster* (e.g. *C. buxifolia*) the carpels become stony and the pome resembles a drupe. In *Cydonia vulgaris* (bihi), quince, there are 5 carpels each with a number of seeds.

III. **Rosoideae.**—Carpels numerous on a convex or conical gynophore, rarely few, not enclosed; or 1-numerous in a concave receptacle; each with 1-2 ovules. Fruit indehiscent.

(*a*) POTENTILLAE.—Receptacle flat or convex, not forming part of fruit, carpels usually numerous on a convex gynophore.

- (i) *Rubinae.*—Carpels with 2 ovules, fruit an etaerio of drupes (Figs. 174, B, 257, B). Includes *Rubus idaeus* (raspberry), *R. fruticosus* (blackberry, bramble) and other species cultivated for their fruits or wild.
- (ii) *Potentillinae.*—Carpels with one suspended ovule, fruits achenes, epicalyx present. Includes the cultivated *Fragaria elatior* (strawberry) and wild species which have numerous small achenes borne on a fleshy receptacle (Fig. 257, C); *Potentilla*, which has a dry receptacle (Figs. 255, B, 256, B). Several species occur in the hills.

(*b*) SANGUISORBEAE.—Receptacle cup-like, containing two or more carpels, hardening in fruit. *Alchemilla* has 4-5 sepals, no petals (Fig. 255, D). *A. indica* has an epicalyx, 4-5 stamens, 1-5 carpels.

(*c*) ROSEAE.—Fruit of many achenes enclosed in a deep, hollow fleshy receptacle (Fig. 174, E). Floral formula, typically K(5) C5 A∞ G∞ (Fig. 256, C). Many roses are cultivated, especially in the hills.

IV. **Prunoideae.**—1 carpel (rarely 1-5), free from the deciduous cup-shaped receptacle (Figs. 174, D, 256, D, 257, E), terminal style, 2 pendulous ovules, fruit a drupe. *Prunus* species are cultivated for their fruits, e.g. *P. persica*, arú, peach with its variety the nectarine; *P. armeniaca*, zardálú, apricot; *P. amygdalus*, bádám, almond, and *P. avium*, cherry. *Pygeum* species are evergreen shrubs and trees.

2. FAMILY **Leguminosae.**—Flowers cyclic, heterochlamydeous, pentamerous usually diplostemonous, hypogynous or slightly perigynous, hermaphrodite, rarely unisexual, actinomorphic or zygomorphic. Carpels usually only one, rarely two, very rarely five to fifteen, with numerous (rarely one) ovules in one vertical row alternating on the two placentae. Stigma terminal. Fruit usually a legume (pod), sometimes indehiscent. Endosperm slight or absent.

This family contains about 12,000 species ranging from arctic to tropical regions. It comprises plants of varied habit, including water-plants, climbers, xerophytes, herbs, shrubs and trees. Many are of economic importance, e.g. for human food, fodder, medicinal use, sources of fibre, dyes, gums, resins, etc. Most species have root nodules (p. 199, Fig. 152) and so can grow in soils deficient in the combined nitrogen required by normal green plants. Hence their great value on poor soils and in rotation of crops.

The plants may climb by tendrils which represent either modified branches, leaves or leaflets; or by hooks which are either emergences (*Acacia*) or leaves (*Caesalpinia*); or they may twine (e.g. lianes), in relation to which the internal anatomy of their stems is modified.

The leaves are usually borne alternately on the stems, are stipulate and, in most cases, compound paripinnate or imparipinnate. The stipules may be leafy or spiny. The leaves may exhibit sleep movements (p. 225) and we have seen that some (*Mimosa*, Fig. 170) are sensitive to touch.

The inflorescence is generally racemose, erect or pendulous. In the latter case the flowers twist through 180° (resupination). The floral receptacle may be convex or flat and the flower, therefore, slightly perigynous.

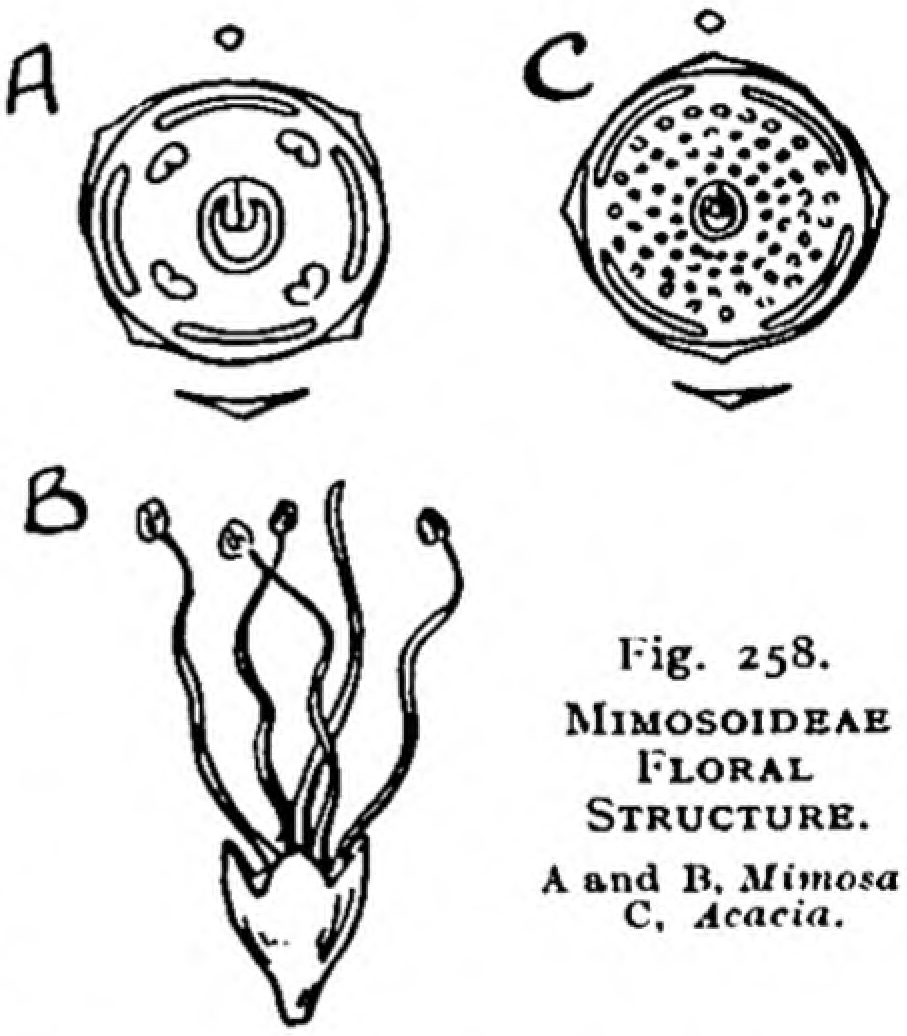

Fig. 258.
MIMOSOIDEAE FLORAL STRUCTURE.
A and B, *Mimosa*; C, *Acacia*.

Three sub-families are recognised, based on differences of floral structure:—

I. *Sub-family* **Mimosoideae.**—Flowers actinomorphic, corolla valvate (Fig. 258), often small. Stamens usually brightly coloured. Leaves mostly compound bipinnate (p. 135), those of *Inga* singly pinnate.

This is the smallest sub-family and includes the genera *Acacia* and *Mimosa*. In *Acacia* the stamens are indefinite and free; in *Mimosa* they are as many or twice as many as the petals and form the most conspicuous part of the flower. Many species of *Acacia* have phyllodes (p. 138) and many have stipular thorns. In *A. sphaerocephala* (Fig. 98, A) the thorns are inhabited by ants which utilise extrafloral nectaries on the petioles, and "food-bodies" at the tips of the leaflets, as food. The ants protect the tree against the depredations of leaf-cutting ants. This symbiosis between ants and plants is known as myrmecophily. In many parts of India, *A. arabica* is the only tree. Its bark, and that of a number of species cultivated in the hills, e.g. *A. decurrens*, is used for tanning. The heartwood of *A. Catechu*, boiled down, is kath
commonly eaten with pán. Cutch or catechu is an extract prepared from the heartwood of this species, and a yellowish tan

is used in the manufacture of khaki. The fragrant flowers of *A. Farnesiana* yield the perfume cassie. Gum arabic is obtained from *A. Senegal* indigenous to northern tropical Africa. *Mimosa pudica,* a Brazilian species, introduced by the Portuguese, has become a troublesome weed in some districts of India. It has extremely sensitive leaves (p. 226). Not quite so sensitive are the leaves of *Neptunia oleracea,* a native water plant with floating stems rooting at the nodes, and *Enterolobium Saman,* the rain tree, introduced from S. America and used as a roadside shade tree. *Albizzia Lebbek,* the sirís, yields a tan-bark and an inferior gum.

II. *Sub-family* **Caesalpinoideae.**—Flowers zygomophic, aestivation of the corolla ascending imbricate (Fig. 259).

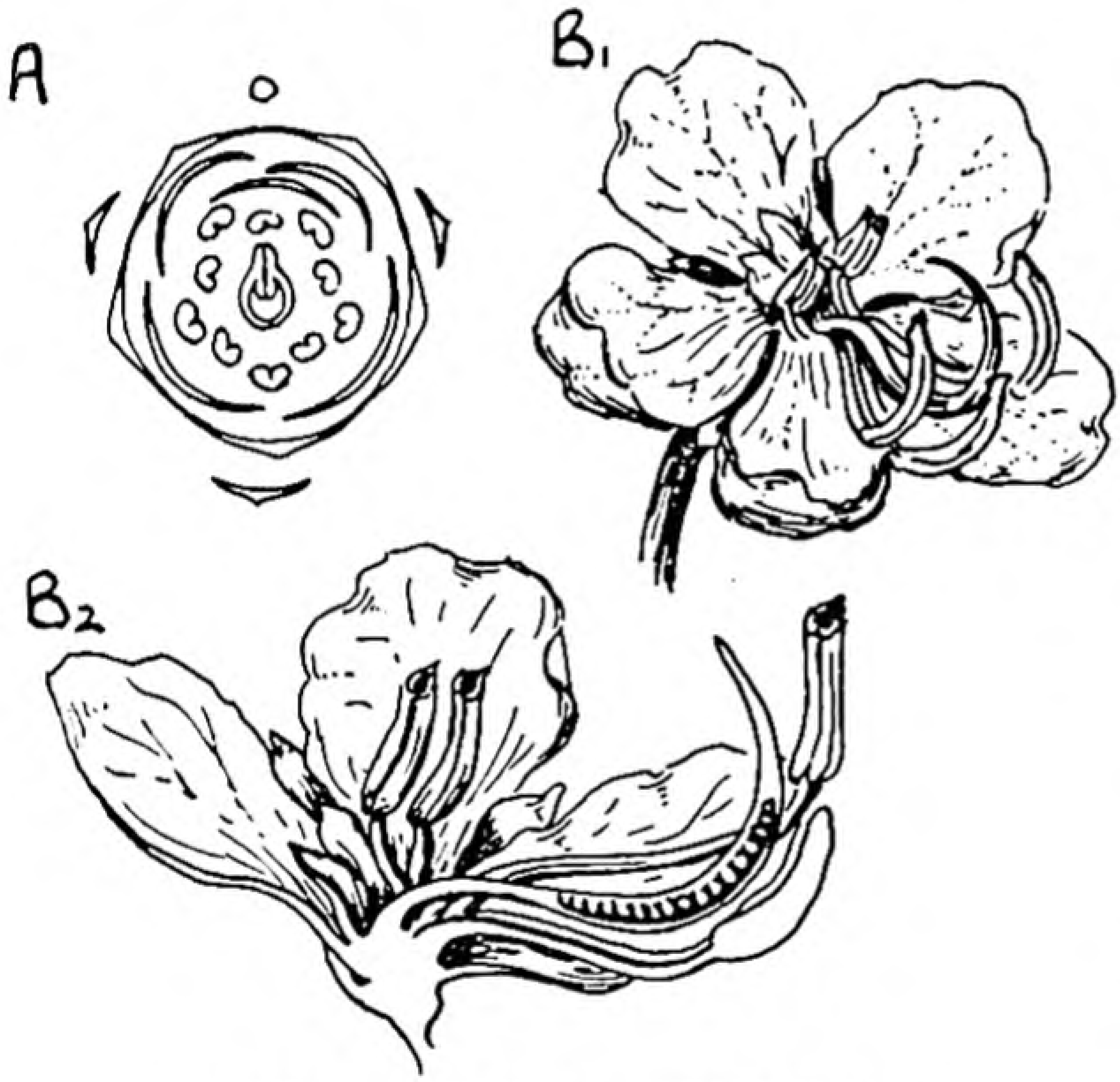

Fig. 259. CAESALPINOIDEAE.
A, *Cercis*, floral diagram ; B, *Cassia*, flower and in section.

Tamarindus indica, probably indigenous to Central Africa, cultivated and self-sown in India, is of some importance. The pod is lomentaceous and has a fleshy mesocarp. It yields tamarinds. The wood has many uses. *Cassia angustifolia* is the Tinnevelly senna, cultivated in S. India for its leaves and pods. *C. Fistula,* the amaltás or Indian laburnum, occurs in the deciduous forests and is also frequently planted. It has long cylindrical fruits which are divided into one-seeded compartments and are indehiscent. These form the cassia pods of commerce. *Caesalpinia Sappan* has a hard, orange-red heartwood, the sappan of commerce. *C. pulcherrima,* the peacock flower, is widely cultivated. The logwood tree, *Haematoxylon Campechianum,* yields haematoxylin, a dye extracted from the heartwood. *Bauhinia* is a large tropical genus; many species are climbers with flattened or twisted stems, and some with "watch-spring" tendrils. The leaves are simple, two-lobed.

III. *Sub-family* **Papilionatae.**—Flowers zygomorphic, aestivation of the corolla descending imbricate (Figs. 177, B, 195, B, and 260).

This is the largest sub-family, so called from its papilionaceous or butterfly-shaped corolla. There are five sepals; the two upper and the three lower are frequently united and the odd sepal is anterior. Of the five petals the posterior forms a large standard (vexillum), the two lateral the wings (alae) and the two anterior the keel (carina). This last encloses the ten stamens whose filaments may be fused to form a tube round the ovary (monadelphous condition, Fig. 195, B), or nine only may be fused and the posterior one free (diadelphous, Fig. 260, C). There is one carpel, sometimes stalked, with a nectar-secreting disc at its base. Some species, e.g. of *Medicago* and *Trifolium*, have only one ovule.

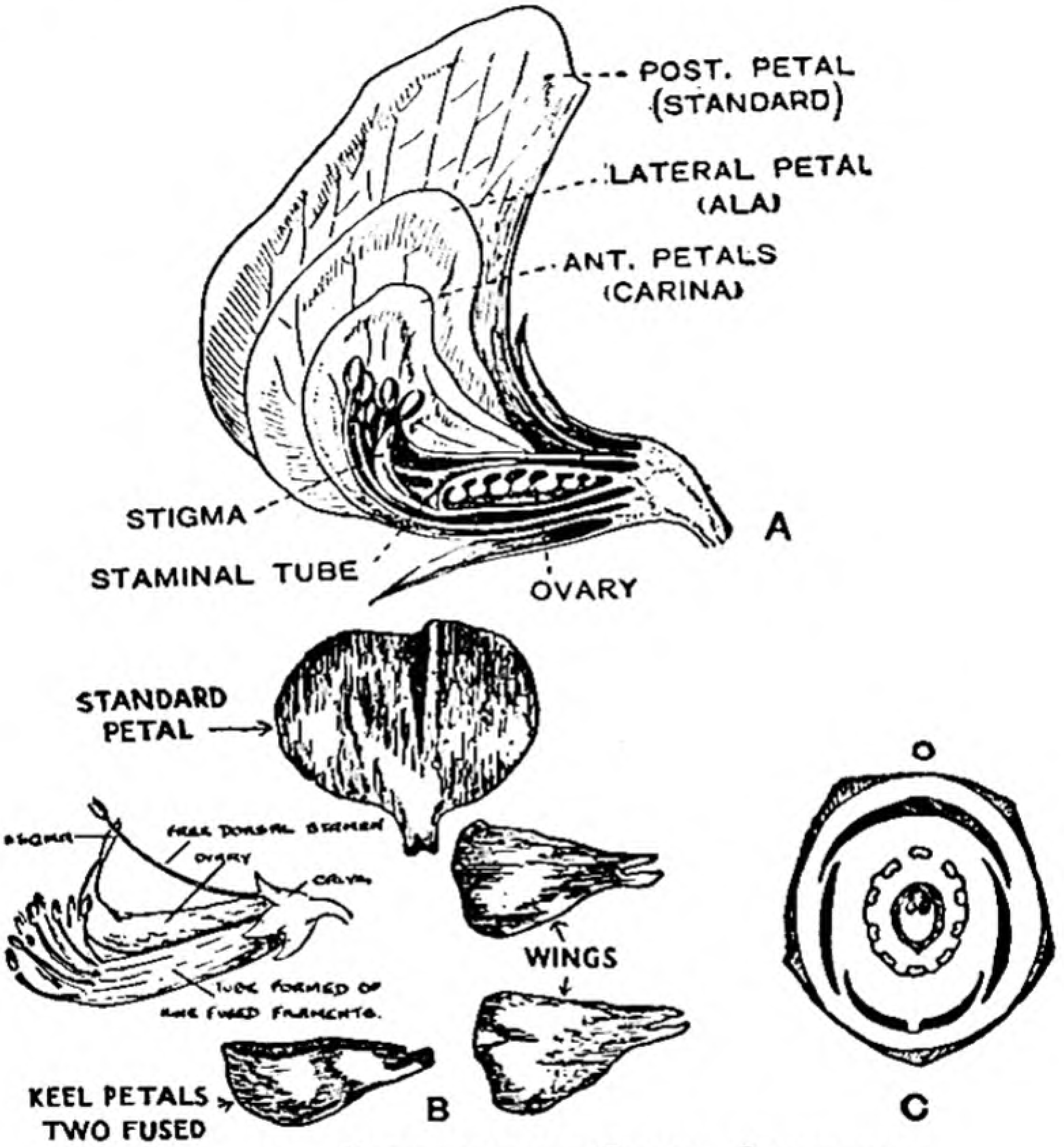
POST. PETAL (STANDARD)
LATERAL PETAL (ALA)
ANT. PETALS (CARINA)
STIGMA
STAMINAL TUBE
OVARY
A
STANDARD PETAL
STIGMA
FREE DORSAL STAMEN
OVARY
CALYX
TUBE FORMED OF NINE FUSED FILAMENTS.
WINGS
KEEL PETALS TWO FUSED
B
O
C

Fig. 260. Papilionatae, Floral Structure.

A, Flower of Pea in vertical section (half-flower); B, ditto, dissected; C, Floral diagram.

Pollination mechanisms have been studied thoroughly in the European genera and are interesting. Where nectar is produced it is secreted between the base of the stamen tube and the ovary, and is accessible only to insects with a long proboscis. Such Papilionatae are bee-flowers. The keel of the flower is more or less horizontal and, with the wings, provides a platform on which the bee can alight. In order to reach the nectar the wings are forced aside, and the keel depressed, thus exposing the anthers and bringing them against the under side of the insect's body where the pollen is deposited. The keel and wings may return to their original position after each insect visit (*Laburnum, Trifolium, Melilotus, Onobrychis*). In other types the insect visit is attended by some sort of explosive mechanism in which all the pollen is spent (*Genista, Medicago, Cytisus*). Sometimes the stigma acts as a piston so that when the keel is depressed, pollen is pushed out at the pointed end against the insect's body (*Lotus, Ononis, Lupinus, Anthyllis*). In other cases the stigma is provided with hairs which act as a brush and sweep out the pollen in small quantities at each insect visit. Here the stigma is receptive only after having been rubbed (*Phaseolus, Pisum, Vicia, Lathyrus*).

Dehiscence of the legume by splitting along dorsal and ventral sutures is frequently accompanied by an explosive mechanism which involves the rapid spiral twisting of the two valves and consequent expulsion of the seeds (Fig. 222, A).

The more important tribes of the Papilionatae are:—

I. **Genistae.**—Leaf simple or palmately divided into 2, 3 or more leaflets with entire margins. Stamens 10, monadelphous. Mostly found in Australia and S. Africa. Many species of *Crotalaria* occur in India, including *C. juncea*, the Sunn hemp, which is cultivated for its valuable fibre. *Ulex europaeus*, gorse or furze, has become naturalised in hilly districts, and two species of broom, *Cytisus albus* and *C. monspessulanus*, natives of the Mediterranean region, are found wild.

II. **Trifolieae.**—Leaves mostly trifoliate, leaflets with serrate margins. Stamens usually diadelphous.

Trigonella Foenum graecum, methí, yields fenugreek seeds. *Melilotus* species occur in some districts as weeds of cultivation. *Trifolium* species, including red, and white or Dutch, clover have been introduced and are useful forage plants.

III. **Galegae.**—Leaves imparipinnate, leaflets entire. Stamens generally diadelphous. Pods dehiscent. Herbs or shrubs. A number of species of *Indigofera* occur in India, but *I. tinctoria*, tropical Africa, and *I. anil*, cultivated in the tropics, are the main sources of indigo. *Psoralea* is another genus represented in India. *Tephrosia* includes herbs and under-shrubs in which the stipules may be modified to spines. Tragacanth comes from species of *Astragalus* occurring in Asiatic Turkey, Persia and Eastern Europe; liquorice root from species of *Glycyrrhiza* distributed over S. Europe to C. Asia.

IV. **Hedysareae.**—Leaves trifoliate or imparipinnate; stamens generally diadelphous, rarely monadelphous; pods lomentaceous if more than one-seeded. Herbs or shrubs, sometimes twining. *Arachis hypogea* (indigenous to tropical America), ground-, monkey- or pea-nut, is largely cultivated. The pod has a fibrous pericarp and ripens underground. The seeds are edible and yield a valuable oil. *Aeschynomene aspera*, the shola, is a shrub growing in shallow water. The lower part of its stem is thickened by the development of a spongy xylem. This tissue, cut into thin strips, is used to make pith helmets or topees. *Desmodium* is a fairly large genus of herbs and shrubs. *D. gyrans*, the telegraph or semaphore plant, is so-called because its two lateral leaflets execute continual rotary movements so long as the temperature is not below 22° C.

V. **Dalbergii.**—Leaves pinnate, stamens monadelphous or diadelphous, pod indehiscent. *Dalbergia latifolia* is the blackwood or East Indian rosewood; *D. Sissoo*, shisham; *Pterocarpus* species yield good timber, *Pt. santalinus* (East Indies) is the source of red sandalwood, *Pt. Marsupium* gives East Indian or Malabar kino. The heartwood of *Andira araraba* (S. America) is the source of chrysarobin. *Derris elliptica* (tuba putch) and *D. malaccensis* (tuba merah), climbing plants indigenous to Malaya, and also cultivated in Malaya, Ceylon and India, are the source of derris root (tuba root, aker-tuba) used as an insecticide. *Dipterix odorata* (Venezuela, Surinam) yields tonka beans, which are rich in coumarin, and are used in perfumery and for flavouring.

VI. **Vicieae.**—Leaves paripinnate, rachis terminating in a bristle or tendril, one or more pairs of leaflets modified as tendrils. Stamens usually diadelphous. Mostly herbs. *Cicer arietinum*, gram, chaná, *Vicia Faba*, broad bean, *Lens esculenta*, lentil, *Pisum sativum*, pea, are all cultivated. *Abrus precatorius*, crab's eye, rati, a climber, has attractive seeds with scarlet and black testas. These are the original carat weight of jewellers and are still used as weights in India.

VII. **Phaseoleae.**—Leaves trifoliate or compound pinnate. Stamens monadelphous or diadelphous. Pod dehiscent. Prostrate herbs, climbers, shrubs, rarely trees. *Glycine Soja*, eastern Asia, yields the valuable soya bean. *Erythrina indica*, the coral tree, is used as a support for pepper. *E. suberosa* has a useful wood. *Mucuna pruriens* is a slender climber whose fruits are densely covered with stiff, yellowish-brown hairs, known in commerce as cowhage. *Butea frondosa*, dhák or pulás, is useful for its gum, Bengal kino, and its seeds. It is also used as a host for the lac insect from which shellac is obtained. Its showy flowers yield a yellow dye commonly used in the Holí festival. The flowers of *B. superba* yield a red dye. *Phaseolus* is an important genus, of which the following species are cultivated: *P. lunatus*, lima bean; *P. vulgaris*, French bean or haricot bean; *P. multiflorus*, scarlet runner; *P. radiatus*, múng; *P. Mungo*, tikari kalai. *Vigna Catjang* is cultivated for its pods which are eaten like French beans, and for its seeds. The pods of *Dolichos Lablab* are also edible, and *D. biflorus*, horse gram, is cultivated for its seeds and for fodder. *Cajanus indicus* is the pigeon pea.

H. ORDER GERANIALES.—Flowers cyclic, heterochlamydeous or apopetalous, rarely quite naked, usually pentamerous. Androecium various. Ovary superior. Carpels 5-2, rarely more, syncarpous, in one whorl, tending to separate from one another when ripe, usually with 2-1, rarely numerous, ovules. Ovules anatropous, pendulous, with ventral raphe and micropyle facing upwards, or, when more than one ovule present some have dorsal raphe and micropyle facing downwards.

1. FAMILY **Rutaceae.**—Flowers 5-4-merous, hermaphrodite, rarely unisexual, actino- or zygo-morphic. Disc circular or cushion-like or cup-shaped. Stamens obdiplostemonous or haplostemonous, occasionally reduced to 3 or 2 by abortion, rarely numerous (possibly by sub-division). Carpels on a gynophore, 5 or 4 (rarely 3, 1 or numerous), sometimes free below and fused above only, usually with 2 ovules per carpel. Fruit and seed various.

This is a large family, more characteristic of the sub-tropical than of the tropical zones, but well represented in India by oranges, limes, etc. They are nearly all trees or shrubs, with alternate or opposite leaves, which are generally compound without stipules. The leaves have oil-glands embedded in them, which show as translucent dots when held up to the light. In *Citrus*, the genus to which belong oranges, limes, etc., the leaf is apparently simple, but the winged petiole is articulated to the lamina, which indicates that it is really one leaflet of a compound leaf (Fig. 109).

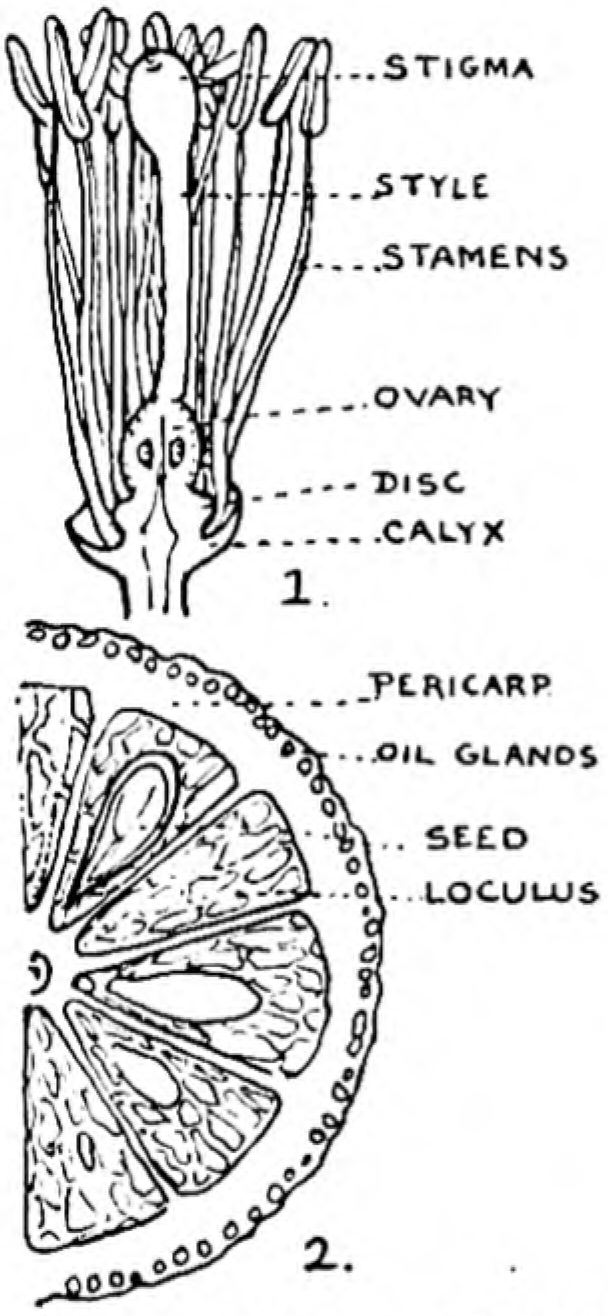

Fig. 261. *Citrus aurantium*.
1, Flower in V.S., petals removed.
2, Half T.S. fruit.

The construction of the **inflorescence** is generally cymose and the **flowers** are most often ☿ and regular, with a large disc below the ovary. The **calyx** and **corolla** have 4 or 5 parts each, and the sepals and petals are free from one another; the **stamens** twice as many or sometimes as many, or ∞, with introrse anthers; the pistil of 4 or 5 carpels syncarpous, **ovary** superior, with as many loculi and axile placentation, and with two or more ovules in each loculus. The **fruit** is of various kinds, a schizocarp, berry, or drupe. That of the orange and lime, for example, is a berry with a leathery epicarp, the flesh made up of cells which grow out from the inner layer of the pericarp (Fig. 261).

The most familiar members of this family in India are the various species and varieties of *Citrus*, such as *C. Aurantium*, the orange; *C. medica*, the citron, with its varieties; *C. Limonia*, the lemon; *C. acida*, the lime; *C. Limetta*, the sweet lime; *C. decumana*, the shaddock or pomelo (chakotrá), etc. *Aegle marmelos* is the bael fruit; *Feronia elephantum*, the elephant apple; *Murraya Koenigii*, the curry leaf (gándhelá), etc.; and there are many wild members of the family, chiefly belonging to the same sub-family, Aurantioideae, as the oranges, etc. The twigs of *Zanthoxylum alatum* (tirmar or tejbal) are used as tooth-brushes. The dried leaves of *Boenninghausenia albiflora* (pissu már, flea-killer) are believed to be effective against fleas. *Chloroxylon Swietenia* is the source of satin wood, valuable for furniture, etc.

2. FAMILY **Euphorbiaceae.**—Flowers unisexual, male or female, often very reduced. The perianth is either absent, of one whorl (calyx) or of two whorls, usually pentamerous. Stamens as many as the sepals, or twice that number, numerous or only one. Carpels 3, fused, rarely 2, 4 or numerous, axile placentation, trilocular. Fruit a schizocarp, often explosive.

Nearly all the plants belonging to this large and interesting family have laticiferous cells (Fig. 26, B) or vessels. Most of them live in warm climates, e.g. the castor-oil plant (*Ricinus communis*) and many species of *Euphorbia* and *Croton*. Shrubs and trees are common amongst these exotic forms, and many of them (e.g. species of *Euphorbia*) show very curious vegetative characters correlated with their environment. In these xerophytic forms the leaves are frequently absent or reduced to spines and the stipules are frequently modified to spines. The stems perform photosynthesis and may form cladodes, or may become swollen and more or less cactus-like and thus serve for the storage of water (Fig. 138, C). Many of the species are poisonous. Perimedullary phloem is present in a number of species.

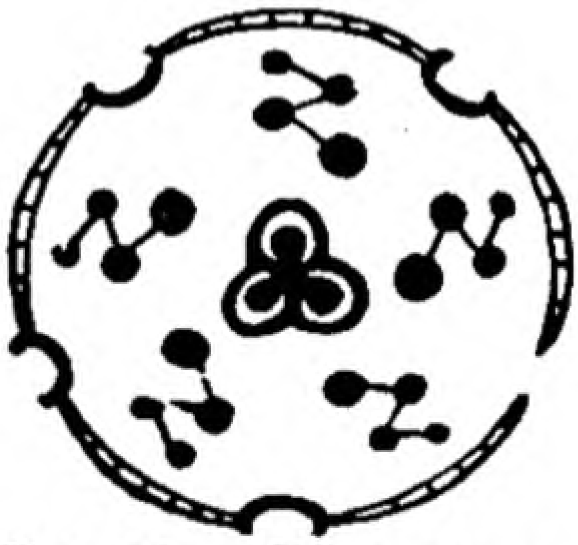

Fig. 262. DIAGRAM OF CYATHIUM OF *Euphorbia*.

The **inflorescences** may be racemose or cymose and are often complex. The **cyathium** is the characteristic inflorescence in *Euphorbia* (Figs. 206 and 262). The **flowers** are unisexual, monoecious, or dioecious, and often much reduced; in *Euphorbia*, for example, the male flower consists of a single stamen.

Occasionally **calyx** and **corolla** are both present and are hypogynous (e.g. species of *Croton*), but frequently the corolla is absent and sometimes also the calyx. **Stamens**, few or many, sometimes one (*Euphorbia*). The **gynaeceum** is the part which shows the most constant characters. It is usually tricarpellary (or bi-carpellary) and syncarpous; the *ovary* is trilocular (or bilocular) and superior; there are one or two pendulous, anatropous ovules in each loculus. The **fruit** is a schizocarp, breaking, often with violence, into dehiscent portions (cocci). The **seed** is endospermous, and frequently has a caruncle developed from the micropyle (e.g. castor-oil seed, Fig. 40).

Many species of *Phyllanthus* are common weeds in India. They possess no latex. The fruit of *P. Emblica*, amlá, rich in tannin, is commonly pickled and also used in medicine. *Croton Tiglium* is indigenous and also cultivated for its seeds which yield croton oil, a powerful purgative. (*C. Eleuteria*, from the Bahama Islands, yields cascarilla bark, used in medicine.) *Hevea brasiliensis*, the source of Para rubber, was introduced from the Amazon region of South America to Ceylon and Singapore in 1876, and since then to other parts of the tropics. By means of suitable incisions and repeated tappings, which induce wound-response, a steady flow of latex is maintained over a long period. This is coagulated, pressed and dried. An average tree, seven years old, yields about 2½ lb. per year. Other species of this genus also yield good rubber. *Mallotus philippinensis* is a small tree widely distributed throughout India, Ceylon, Malay, etc. Its fruits are covered with glands and hairs which form the kamala (wars) of commerce, collected chiefly in Orissa, Bengal and Bombay, and used as a vermifuge. *Ricinus communis*, castor-oil plant, a native of Africa, grows wild and is cultivated in India. The stamens are much branched, the fruit explosive, and the seeds yield castor-oil, much used in medicine and also as a lubricant (see p. 61). *Codiaeum variegatum*, "croton" of gardens, is familiar for its attractively coloured variegated leaves which are also often peculiarly shaped, in that portions of naked petiole separate different parts of the lamina. *Manihot Glaziovii* yields the ceara rubber of Brazil. It is not widely cultivated because, although it reaches the producing stage sooner than *Hevea*, the yield of rubber is not so high. *M. utilissima* is the bitter, and *M. Aipi* the sweet, cassava or manioca. Their tuberous roots contain much starch and form valuable foods. The former contains prussic acid when fresh, but this is driven off by boiling or roasting. In some countries the starch is made into tapioca by being carefully washed and then gently heated while still wet. *Euphorbia* is represented by many species in India. It includes small herbaceous plants and large cactus-like species, e.g. *E. Royleana* and others which have fleshy angled stems, and occur in dry places. *E. tirucalli*, the milk hedge, was introduced from tropical Africa, but is quite common. It has thin cylindrical stems.

In *E. splendens* the cyathia are rendered conspicuous by the bright red larger upper bracts. *E. resinifera*, Morocco, yields euphorbium, an acrid resinous substance consisting of the dried latex.

I. ORDER SAPINDALES.—As the Geraniales, but the ovules in the reverse position, either pendulous with dorsal raphe and micropyle facing upwards, or ascending with ventral raphe and micropyle facing downwards.

1. FAMILY **Anacardiaceae.**—Flowers usually pentamerous, diplostemonous or haplostemonous, rarely with fewer or more stamens. Carpels usually (3-1) rarely (5), with one pendulous or ascending anatropous ovule. Fruit various, usually with a stony mesocarp. Endosperm absent or slight. Embryo frequently curved with flat or plano-convex cotyledons. Trees and shrubs, usually with acrid or resinous schizolysigenous glands; leaves spiral, rarely opposite, simple or trifoliate or imparipinnate. Flowers numerous, small, in panicles. Warm to temperate regions.

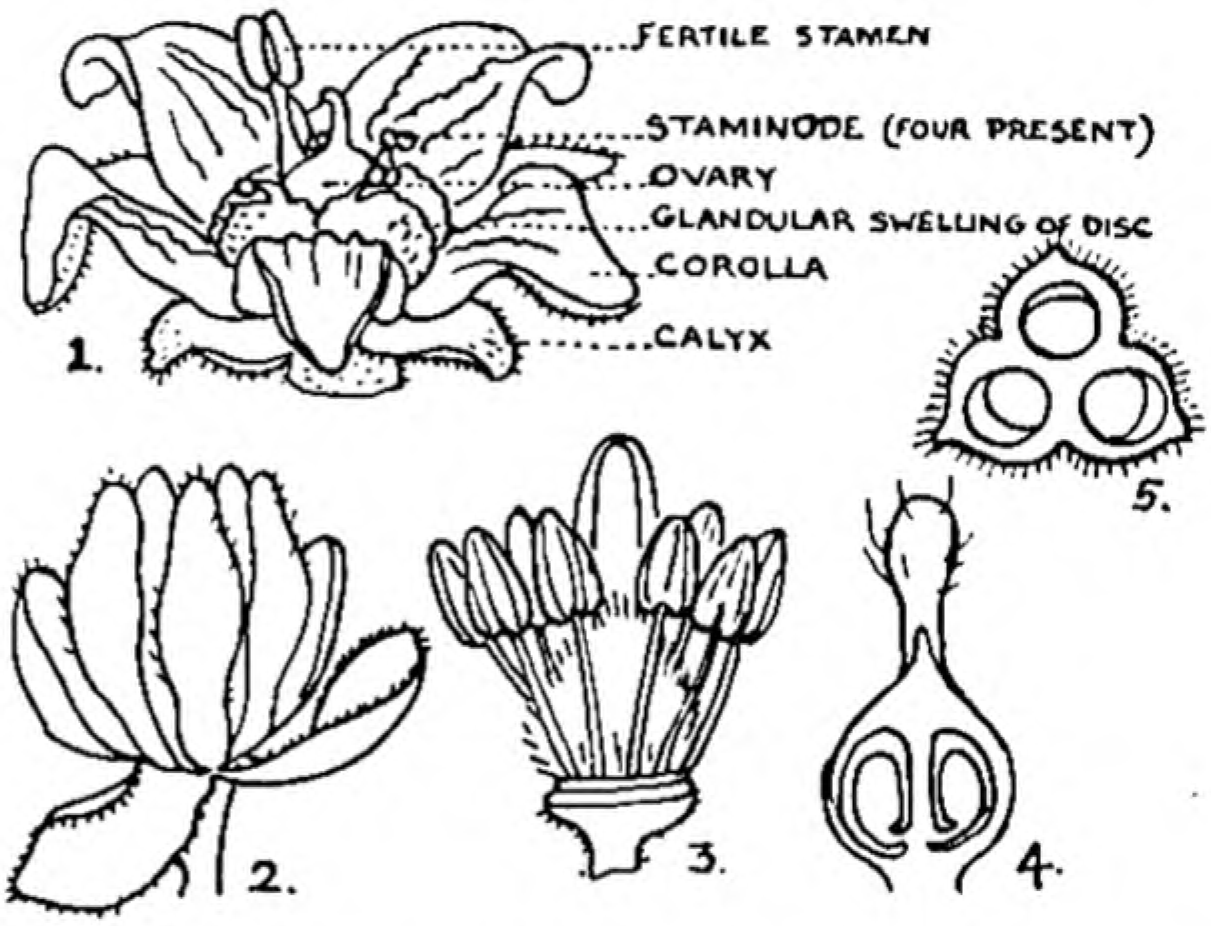

Fig. 263. *Mangifera* AND *Sapindus*.

1, *Mangifera indica*. Flower; 2-5, *Sapindus emarginatus*; 2. Flower with sepals displaced to show insertion of petals; 3. Stamens and pistil of a hermaphrodite flower; 4. Ovary in L.S.; 5. Ovary in T.S.

Mangifera indica, the mango (Fig. 263, 1), is widely cultivated for its edible fruit which is a large, fleshy drupe with a compressed fibrous stony endocarp. The fruit is eaten fresh or made into preserves or pickles. *Anacardium occidentale*, the cashew nut, káju, is a native of America, cultivated and naturalised in India. The fruit is a reniform nut seated on a large pyriform fleshy body formed of the enlarged floral disc and top of peduncle. The kernels are eaten and the pericarp yields an acrid caustic oil. *Spondias dulcis* (Polynesia) and other species of hog-plum are cultivated for their fruits. *Pistacia vera* (Mediterranean) yields pistacia nuts, pista; (*P. Terebinthus*, chian turpentine, *P. Lentiscus*, mastic). *Rhus* species are rich in tannin [*Rh. Coriaria* is the sumach; *Rh. Toxicodendren*, the poison ivy of N. America; *Rh. Cotinus*, Mediterranean to China, the wig-tree, so named because the sterile parts of the panicle become very hairy and aid in the dispersal of the fruits (drupes) by wind; *Rh. succidanea*, Eastern Asia, and

Rh. vernicifera yield Japanese lacquer, and the former Japanese wax from its berries.] *Semecarpus* species contain a useful black resin. *S. Anacardium* bears seeds known as bhiláwá whose juice is used in marking cotton clothes.

2. FAMILY **Sapindaceae.**—Flowers typically pentamerous, rarely actinomorphic, usually obliquely zygomorphic, with an extra-staminal, prominent, one-sided disc. Corolla 5-3 or 0, frequently with appendages. Stamens usually 8, rarely 10, 5 or numerous. Carpels (2-3), usually with 1, rarely 2 or more ovules (Fig. 263, 2-5). Fruit a capsule, nut, berry, schizocarp or samara. Seeds often with a large arillus rich in sugar, non-endospermous. Embryo curved.

Most of this large tropical family consists of trees and shrubs, but *Cardiospermum*, which is very common, is herbaceous, and there are a few climbers, which mostly have peculiar hooks, composed of modified inflorescence axes, which thicken after clasping. The **leaves** are alternate, and have stipules in the climbing species; they are generally compound and pinnate, and sometimes have a terminal leaflet, but sometimes have one of the pair of end leaflets of a paripinnate leaf bent round to a terminal position.

The **inflorescence** is cymose, and the flowers, though they generally appear as if hermaphrodite, are really unisexual, for the anthers are often well developed in the female flower, though containing no good pollen. The **flowers** are regular or zygomophic; the **sepals** and **petals** are 5 or 4, the former sometimes, but rarely, united. The **stamens** are usually twice as many, but often two are absent, and sometimes they are only 5 or 4, or may even be ∞. The **ovary** is superior, usually of three carpels, trilocular, with a terminal style, and one ovule in each loculus. The **fruit** is perhaps most often dry—a capsule or nut—but berries and drupes are not uncommon. Often the nut has wings and becomes a samara.

Several Sapindaceae of Indo-Malaya give useful fruit, especially *Nephelium lappaceum*, the rambutan, and *N. longana*, the longan. The litchi of China, *Litchi chinensis* (líchí), is often cultivated in India. The edible part of the fruit in these three species is the fleshy arillus, which is enormously enlarged and completely surrounds the seed. Many Sapindaceae yield valuable timber. The fruit of *Sapindus Mukorossi* and *S. laurifolius* is the rítthá or soap-nut, the pericarp of which is widely used in India as a useful substitute for soap, especially for washing woollen and silken clothes. *Dodonaea viscosa* (sanatta, kharata) grows wild over large areas of dry uncultivated land in North-West and Central India, as well as in the Deccan, and is also frequently planted in hedges. The leaves are covered with a viscid resinous secretion, and the fruit is three-winged.

3. FAMILY **Balsaminaceae.**—Flowers hermaphrodite, K5 or 3, the two anterior often reduced or aborted, the posterior one spurred. C5, the two lateral petals fused in pairs. A5, G(5), 5-locular

each with numerous ovules. Capsule explosive, seeds numerous, non-endospermous, embryo straight.

This family consists of the genus *Impatiens*, the Balsam, which is one of the characteristic genera of the Indian flora, occurring in all the hilly regions in great profusion, each group of hills being principally occupied by species confined to that group, or endemic to it. They are herbs with watery translucent stems, alternate exstipulate leaves, and zygomorphic flowers (Fig. 264). The sepals are petaloid, and usually very irregular.

The five **stamens** have their anthers united to form a cap over the ovary, and, as the latter grows, the stamens break at the base and the whole cap falls off. The capsule is explosive; it is turgid when ripe in such a way that each of the segments, when they ultimately separate, rolls up inwards with a jerk, throwing out the seeds.

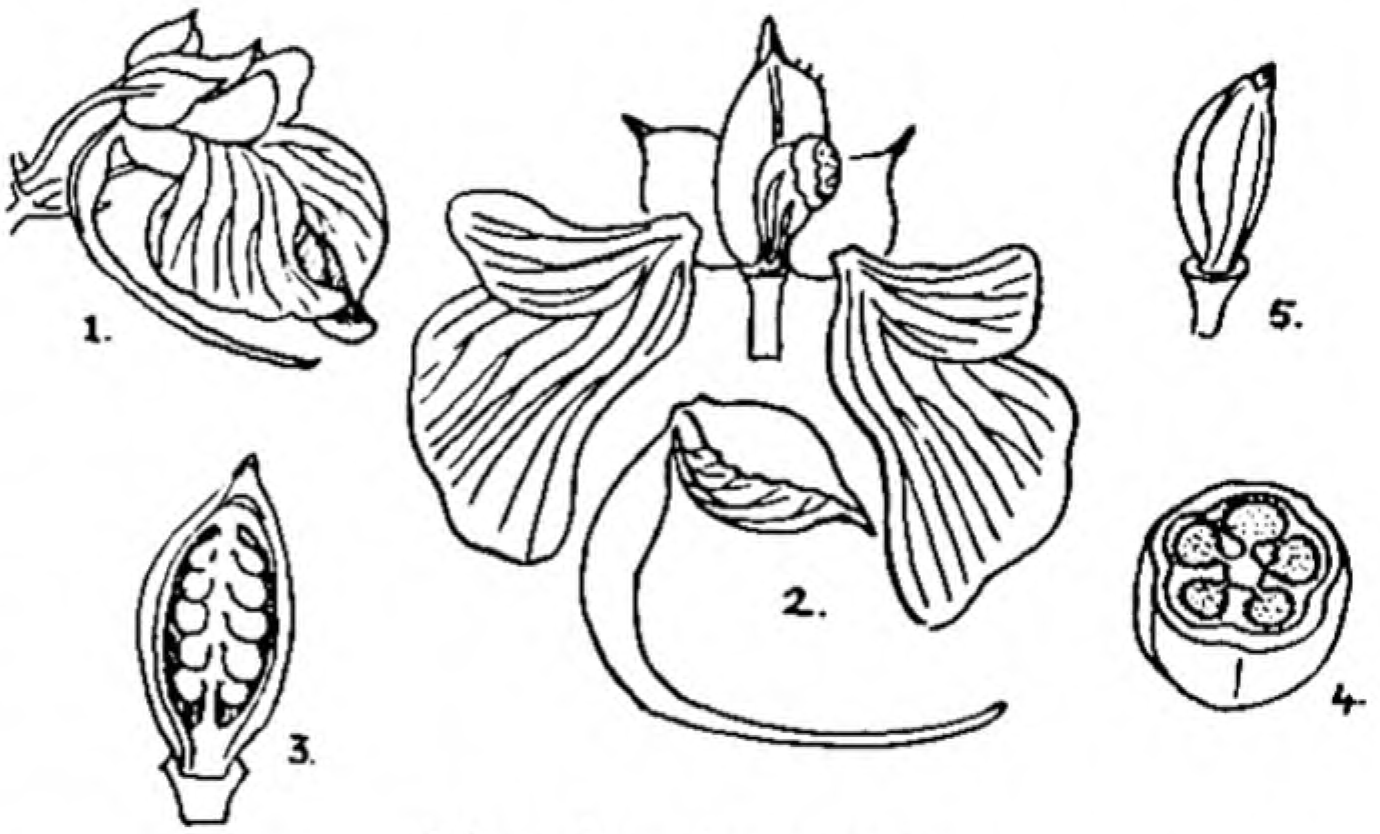

Fig. 264. *Impatiens*.

1. Flower entire; 2. Flower dissected; 3. Ovary in L.S.; 4. Ovary cut transversely; 5. Ovary entire.

J. ORDER MALVALES.—Flowers cyclic (not always in the androecium), heterochlamydeous, rarely apopetalous, hermaphrodite, rarely unisexual, actinomorphic, rarely zygomorphic. Calyx and corolla usually pentamerous. Sepals usually valvate. Stamens numerous or in two whorls of which the inner is divided. Carpels 2 to numerous, syncarpous with one to numerous anatropous ovules.

FAMILY **Malvaceae.**—Flowers usually hermaphrodite. Calyx and corolla pentamerous. Petals twisted in the bud. Stamens very rarely five, usually numerous in two whorls, those opposite the sepals often staminodial, those opposite the petals frequently split, all united in a bundle, anther monothecous with large, spiny microspores. Carpels 5 to numerous, syncarpous, one to numerous ovules, stigmas as many or twice as many. Fruit a capsule or schizocarp. Embryo usually curved, surrounded by endosperm.

Plants representing this family are widely distributed in tropical and temperate regions. *Hibiscus rosa-sinensis* is cultivated. *Gossypium* is the cotton plant. Many are common weeds.

The plants are herbs or shrubs with alternate, stipulate, multicostate leaves. The **flowers** (Fig. 265) may be solitary or in cymose inflorescences. They are regular, hermaphrodite, hypogynous, and usually protandrous.

Calyx usually gamosepalous and five-fid; valvate. An epicalyx is usually present, consisting of three or more leaves representing bracteoles and their stipules (see p. 236). **Corolla** regular, polypetalous, usually of five petals, which are usually asymmetrical and adherent to the base of the staminal tube, twisted in aestivation.

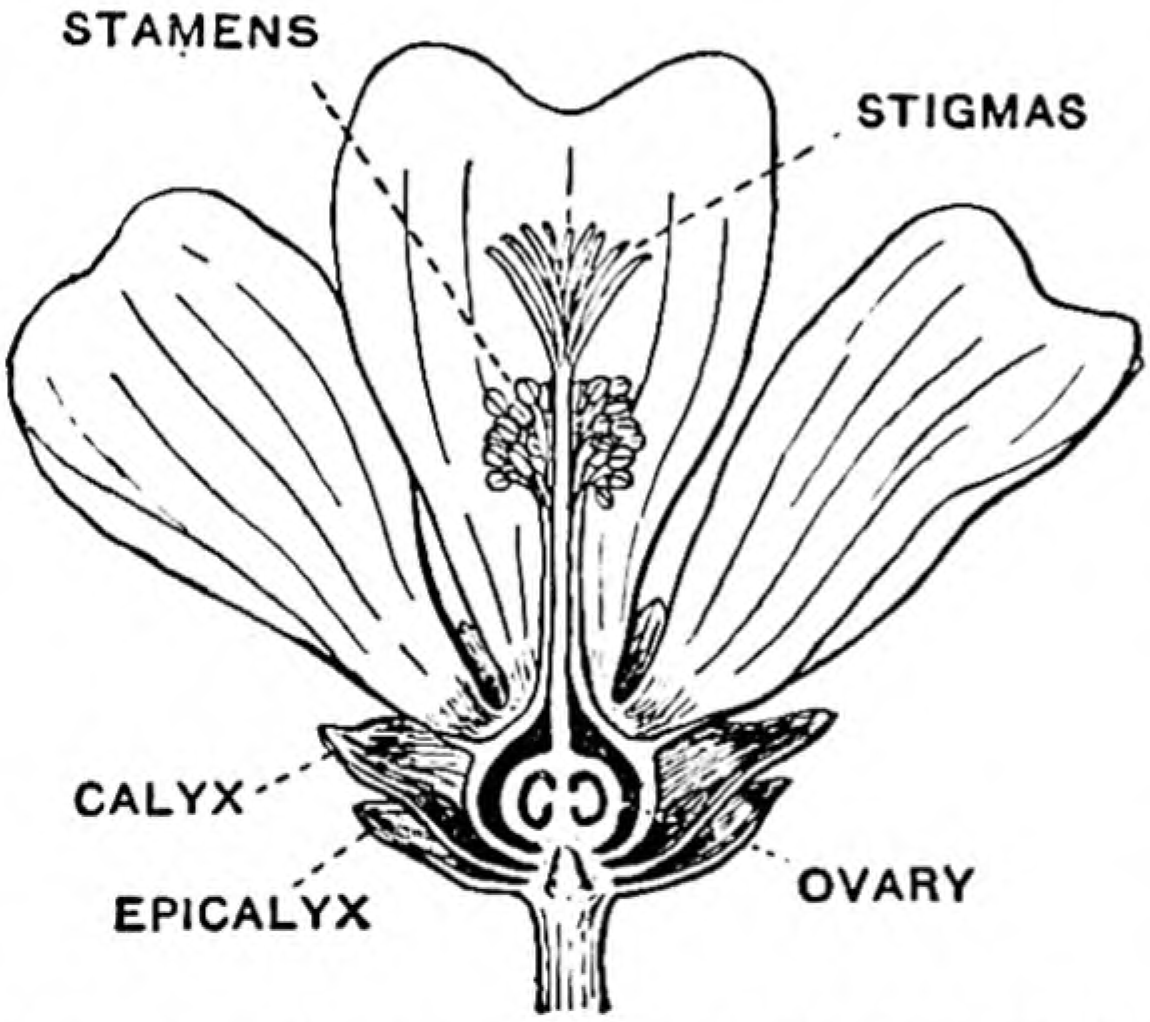

Fig. 265. VERTICAL SECTION OF FLOWER OF SPECIES OF *Malva*.

Stamens ∞ and monadelphous, bearing half-anthers. They are derived by the copious branching of five antipetalous stamens and are united below into a tube fused with the base of the corolla and making it appear gamopetalous; five antisepalous stamens, which have been lost, are still sometimes represented by staminodes (*Hibiscus*). The anthers have transverse dehiscence. **Gynaeceum** polycarpellary (5—∞), syncarpous (occasionally almost apocarpous); *ovary* superior, multilocular; placentation axile; ovules 1—∞ in each loculus; styles united; stigmas free.

Fruit (Fig. 266) usually a carcerulus (see p. 276), splitting into as many mericarps as there are carpels, or a many-seeded capsule (*Hibiscus, Gossypium*). **Seed** with scanty endosperm, sometimes with hairs on the testa, e.g. in *Gossypium*, where the hairs constitute cotton.

Floral formula: $\mathrm{K}(5)\ \overparen{\mathrm{C}5\ \mathrm{A}\infty}\ \mathrm{G}(\underline{\infty})$.

In the different species of mallow the overlapping petals form a convenient landing stage for a variety of insects, chiefly bees. Nectar is secreted by the receptacle in five little pits lying between the bases of the petals and protected by hairs. Some species, however, e.g. *M. rotundifolia*, which is nearly homogamous, are often self-pollinated by the curling over of the stigmas.

Most of the familiar plants of this family in India are garden plants, such as *Hibiscus rosa-sinensis*, the shoe-flower, so called from the use of the petals in polishing shoes; they are also used in colouring stewed mangoes and other fruits. This plant is very variable, and also lends itself readily to hybridisation with *H. schizopetalus* and other species, and a large number of cultivated forms are known.

Several other species of *Hibiscus* are also in cultivation, such as *H. Sabdariffa*, the rozelle, whose calyx becomes fleshy round the fruit, with a pleasant acid taste, which causes it to be largely used for jellies; *H. esculentus*, whose half-ripe fruits, bhindi (lady's finger) are very slimy when cooked and are largely used as vegetables and in soups; *H. tiliaceus*, common on the sea coast, whose bark yields a very strong fibre; *H. cannabinus*, Deccan hemp, cultivated for the sake of the fibre of the bark, etc. Many Abutilons are also cultivated, as well as *Althaea rosea*, the hollyhock (gulkhairá), *Thespesia populnea*, sometimes called the tulip-tree (not to be confused with *Liriodendron tulipifera*, Magnoliaceae), and others, while there are many species of *Sida*, *Urena*, and other genera among the commonest weeds; many of these yield good fibre. Several of the family are important in cultivation, more especially the cotton (*Gossypium*), of which several species are cultivated in India, *G. herbaceum* being generally regarded as the most common, whilst *G. arboreum*, the tree cotton is everywhere grown in small amount.

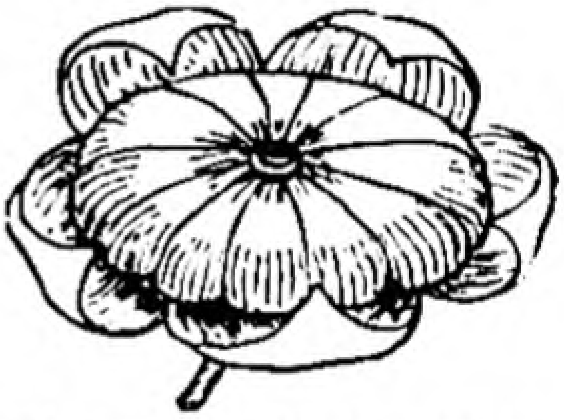
Fig. 266. CARCERULUS OF *Malva*.

The following are now separated from the Malvaceae by Engler, and placed in the family Bombacaceae:—

Eriodendron anfractuosum, a small tree with horizontally spreading branches, is the silk-cotton or kapok; the silky cotton is not, as in *Gossypium*, an outgrowth of the testa, but of the inner wall of the capsule, becoming separated from this when ripe; it is largely used for stuffing pillows. The similar cotton of *Bombax malabaricum*, the red cotton tree, is sometimes used, but rarely, being so high above the ground that it is difficult to reach. This tree is very striking in the months of December, when it loses its foliage, and January, when it bursts into a blaze of scarlet flowers upon the naked branches. The ripe seeds, surrounded by the cotton, fall in April, when the young leaves are coming out. *Adansonia digitata*, baobab, is found in a few localities and is supposed to have been introduced from Africa; it has a short but very thick swollen stem, sometimes as much as 20 feet in thickness and more or less egg-shaped, in which it stores water. The seeds are about 30 in a pouch-like fruit, which is often known as Judas' bag; it is woody, and contains a pulp in which the seeds are embedded.

K. ORDER PARIETALES.—Flowers spirocyclic or cyclic, commonly with numerous stamens and carpels, heterochlamydeous, rarely apopetalous, hypogynous to epigynous, carpels more or less syncarpous, frequently with parietal placentae, which, however, may meet in the middle of the ovary, very rarely with one basal ovule.

1. FAMILY **Dilleniaceae.**—Flowers hermaphrodite, rarely unisexual, actinomorphic, sometimes zygomorphic, frequently, however, partly spiral. K3-8, C5-2, A∞, rarely 10 or fewer, G∞-1, with 1-∞ erect anatropous ovules with ventral raphe. Fruit dehiscent or indehiscent, fleshy or an etaerio of follicles, seed with funicular aril, endospermous.

This is a small tropical family, mostly represented in the scrub vegetation of northern Australia, but with a few common plants in India. Most are trees and shrubs, sometimes climbing, with alternate, usually leathery leaves, and cymes of flowers.

Dillenia indica (Fig. 267, A) is perhaps the commonest species; it is a tree with large white flowers, which are succeeded by large apple-like fruits (chaltá). The fruit is capsular and enclosed in the greatly enlarged and succulent sepals, which are edible. When cut, the fruit gives a lather with water, and is used in washing, especially for the hair. Some species of *Acrotrema* occur in the south.

2. FAMILY **Dipterocarpaceae.**—Flowers hermaphrodite, actinomorphic. K5, C5 convolute, free or fused at the base, A∞ or 15, 10, 5; G(3-1) each loculus with 2 ovules. Fruit usually a 1-seeded nut enclosed in the persistent calyx of which 2, 3 or all 5 sepals form a wing aiding dispersal. Seeds non-endospermous (Fig. 267, B).

This family of 16 genera is a characteristic one of India. The trees are lofty with relatively few branches and entire, leathery, stipulate leaves. They flower but rarely, and the flowers are usually sweet-scented, in racemes or panicles. They contain resin ducts and mucilage cells. Several species of *Dipterocarpus* furnish useful resins or gum-resins, e.g. gurjun balsam, used in medicine and for technical purposes. Some form almost pure forest and yield valuable timber. *Dryobalanops aromatica*, Sumatra and Borneo, yields a kind of camphor. *Shorea robusta*, sal, furnishes timber valuable for building purposes and railway sleepers. *Hopea* species also furnish valuable timber. *Vateria indica* is the piney varnish or Indian copal tree. Its seeds give an oil.

3. FAMILY **Caricaceae.**—Flowers unisexual, actinomorphic, with tubular or bell-shaped axis. Petals 5, fused, with a long (male flower) or short (female) tube. Stamens 10, Carpels (3-5) with numerous ovules, parietal placentation. Fruit a berry. Seeds numerous, endospermous. Leaves simple or palmate or pinnate, without stipules and with axillary inflorescences. Numerous thickened, articulated latex-tubes.

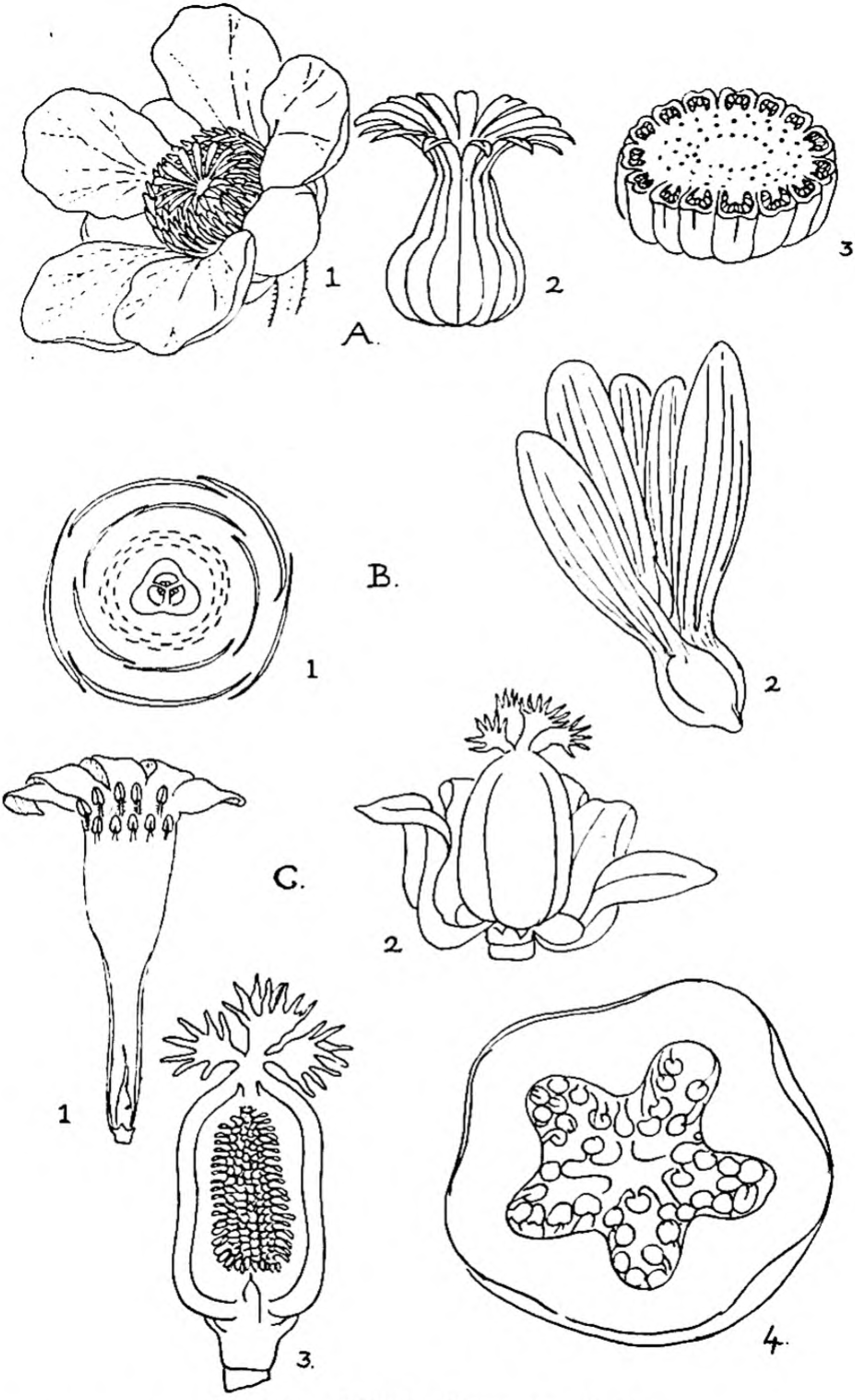

Fig. 267. *Dillenia*, *Shorea* AND *Carica*.

A, *Dillenia*, 1, Flower; 2, Ovary; 3, Ovary in T.S.; B, *Shorea*, 1, Floral diagram; 2, Fruit; C, *Carica*, 1, V.S. Flower; 2, Developing fruit; 3, L.S. same; 4, T.S. Fruit.

This family is not indigenous to India, but is represented by the widely cultivated papaw. It consists of small trees with a characteristic palm-like habit of a more or less unbranched stem and a crown of leaves. *Carica Papaya*, the papaw (Fig. 267, C), is unknown in the wild state, but a number of forms occur in Central America, and it is cultivated throughout the tropics for its edible fruit (papayá). The leaves and unripe fruits have a milky juice and contain papain, a protease (see p. 189). If meat is wrapped in the leaves, or rubbed with the juice of the unripe fruit, and buried, a partial digestion of the fibres renders the meat more tender. The fruit is a large fleshy berry resembling a melon.

L. ORDER OPUNTIALES.—Flowers hemicyclic, heterochlamydeous. K, C and A ∞, spiral on a tubular axis. Ovary inferior.

FAMILY **Cactaceae.**—Flowers hermaphrodite, actinomorphic, occasionally somewhat zygomorphic, generally brightly coloured, often with a long tubular receptacle. Stamens ∞. Carpels (4-8). Stigma 1. Ovary usually unilocular with ∞ ovules and parietal placentation. Fruit a berry with numerous seeds. Embryo straight or curved with sometimes very small cotyledons. The plants are mostly succulent, sometimes epiphytic, rarely with flat or cylindrical leaves, as a rule with fleshy stems having apparent longitudinal ridges (orthostichies) or cushion-like swellings; leaves usually fall prematurely, leaf-cushions usually felt-like and furnished with spines which probably represent the modified leaves of the axillary branches. Flowers usually borne on the leaf-cushions, bird or insect pollinated. About 1500 species, mostly in temperate to warm regions of America, few (doubtfully native) in Africa, Madagascar and the Old World. The most widely distributed member of this family is the epiphytic *Rhipsalis cassytha* (Fig. 268), found in Ceylon. Certain opuntias or prickly pears are quite common in the East, especially in dry places and on the sea beach, but they have been introduced and some have become noxious weeds. The family shows on the whole most pronounced xerophytism, in that the surface exposed to the air is greatly reduced, the cuticle thick, and a large amount of water is stored in the fleshy tissues.

In the opuntias the stems are flattened, and each successive joint grows out as a branch on the one which preceded it. The surface is generally covered with little groups of spines, arranged according to a definite phyllotaxy; these are usually regarded as the leaves of the axillary shoot due to appear at this point. The leaves of *Opuntia* appear early and are small, whilst they only function for a very short time in most species, and drop off, leaving the fleshy green stem as a photosynthetic organ. In many of the Cactaceae the stem is angular, and is comparable with that of one of the large fleshy species of *Euphorbia* that are so common in India, but the cactus stem bears its thorns in little groups, the *Euphorbia* generally in pairs.

The **fruit** is a berry, with the flesh formed by the growth of the stalks of the ovules. It is often edible, though care must be taken to avoid the thorns.

M. Order MYRTIFLORAE.—Flowers cyclic, heterochlamydeous, rarely apopetalous, haplostemonous, or diplostemonous (frequently associated to form a column), rarely zygomorphic, with more or less concave axis and 2-numerous carpels, syncarpous, rarely free, usually united to the axis (receptacle), and inferior rarely with one free carpel.

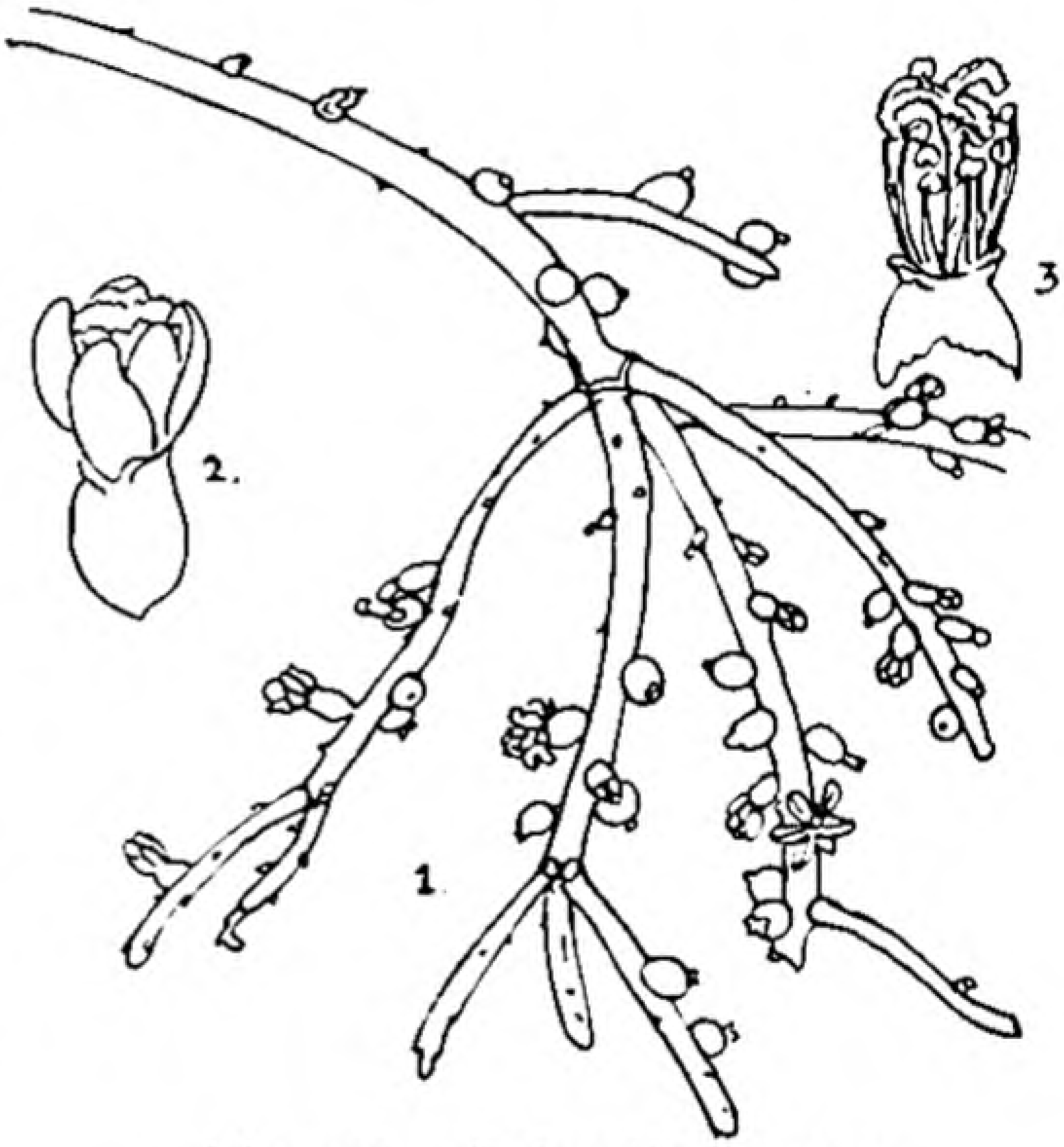

Fig. 268. *Rhipsalis cassytha.*
1, Habit; 2, Flower; 3, Same with petals removed.

Family **Myrtaceae.**—Flowers heterochlamydeous, hermaphrodite, actinomorphic. K and C usually 4-5, free or fused. Stamens ∞, frequently fused in groups, rarely definite, often coloured. Carpels 2-5-∞, syncarpous, fused with the receptacle (inferior), axile placentation, with 8-1 anatropous or campylotropous ovules per loculus. Stigma 1. Fruit various. Seeds usually non-endospermous.

This is a large family, well represented in the tropics, especially by cultivated plants, which include the jambulams, guavas, eucalypti, etc. They are trees and shrubs, sometimes climbing, and usually have oil glands in the leaves which may be recognised by holding them up to the light, when the glands show as clear spots. The leaves are generally opposite, exstipulate, evergreen and entire. There is often a so-called infra-marginal vein. Perimedullary phloem is present.

The **flowers** are usually in cymes, the receptacle hollow and united to the ovary, the flower being in consequence epigynous.

In some genera the union is not complete (e.g. *Metrosideros*). The **calyx** is sometimes thrown off as a cap on the opening of the flower, instead of opening in the ordinary way; the **petals** are often nearly circular, and sometimes thrown off bodily as a cap on opening; the **stamens** are usually bent inwards in the bud (Fig. 269). Pollination is by insects or birds.

Among the native or cultivated forms in India are the various jambulams, some native, some of Malayan origin, all species of *Eugenia*, with fleshy fruits, which are edible, though not specially attractive. Among them are *E. malaccensis*, the Malay apple, *E. Jambos*, the jambu or rose-apple, the South American *E. Michelii*, the Brazil cherry, and many others. *Eugenia caryophyllata*, a Malayan species, furnishes the cloves of commerce (lavang), which are the dried flower buds (Fig. 269). The genus *Eugenia* is characteristic of the flora of the hills of southern India and Ceylon, occurring in each group of hills in many species, the Ceylon mountains, for example, possessing 43 species, of which 29 are endemic, or confined solely to that group of hills.

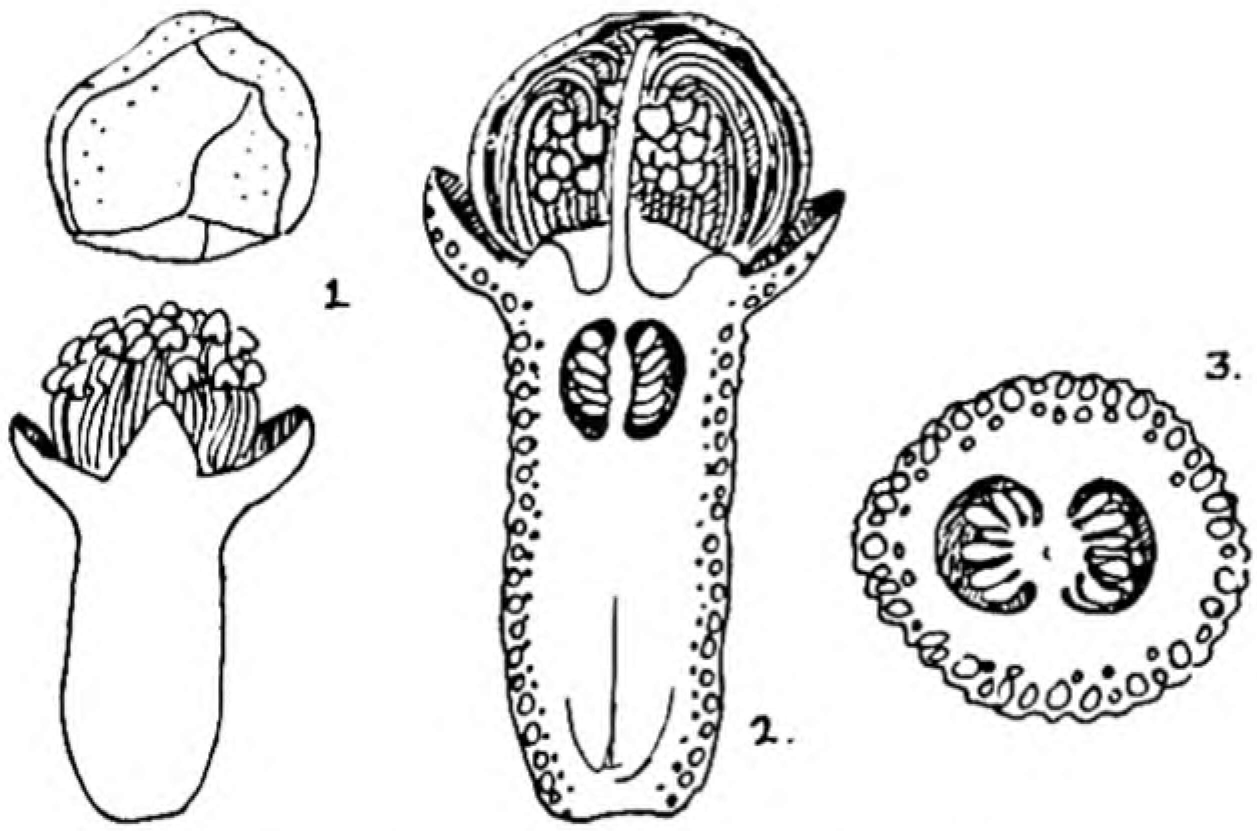

Fig. 269. *Eugenia* (Clove).

1, Flower, with petals removed; 2, Flower bud in V.S.; 3, T.S. Ovary.

Rhodomyrtus tomentosa, the hill guava, or hill gooseberry, is another common plant along the edges of patches of forest in the hills. The various guavas proper are species of *Psidium*, mainly introduced from tropical America by the Portuguese; the commonest, now a troublesome weed on much waste ground, is *P. Guayava*, the guava *par excellence*, which makes an excellent jelly.

Among the best known plants of this family are the various species of *Eucalyptus* which are so much planted in the hills, but which are really natives of Australia, where they form a characteristic feature in the landscape. The best known of them is perhaps *E. globulus*, the blue gum, which in the younger parts has bluish-coloured cordate, sessile, opposite leaves on square branches, while in the older parts it has greenish scimitar-shaped, stalked, alternate leaves, twisted into the vertical plane on round branches. Cultivated species are *E. leucoxylon*, the ironbark; *E. robusta*, the swamp mahogany; *E. marginata*, the jarrah (which yields the resistant timber employed in paving the streets of cities), and others. Many of the gum trees, as the Eucalypti are commonly called, yield a valuable timber, others give kino red gum, and several yield the well-known eucalyptus oil by distillation of the leaves.

Pimenta officinalis, West Indies, yields allspice.

N. ORDER UMBELLIFLORAE.—Flowers cyclic, heterochlamydeous, usually haplostemonous, epigynous, 4-5, rarely polymerous, usually hermaphrodite, actinomorphic or zygomorphic. Carpels 5-1 or numerous, syncarpous, with 1 (rarely 2) pendulous anatropous ovules with one integument. Seeds rich in endosperm. Flowers usually in umbels.

FAMILY **Umbelliferae.**—Flowers pentamerous, haplostemonous, often with indistinct calyx and two median carpels, usually hermaphrodite, actinomorphic frequently zygomorphic. Ovary bilocular. The two styles at their base swell into an epigynous disc (stylopodium). Fruit a schizocarp (cremocarp) splitting into 2 mericarps which remain suspended on the carpophore for a time.

This is a very large and important family, easily recognised by the general habit of the plants and their fruits. The plants are either herbs or shrubs with hollow (fistular) stems and alternate, amplexicaul, exstipulate leaves, which are usually much divided.

The **inflorescence** is usually a compound umbel (Fig. 203), occasionally a simple umbel. These umbels are sometimes cymose in character, and a terminal flower may occur as in the wild carrot (*Daucus Carota*). The **flowers** (Fig. 188) are usually hermaphrodite and regular; but unisexual flowers sometimes are found, and frequently the outer flowers of the umbel are irregular and zygomorphic.

The **calyx** is small, consisting of five minute sepals, or absent. The **corolla** is polypetalous; the five petals are usually white or yellow, and often have reflexed tips. The **stamens** are five in number and epigynous. The **gynaeceum** is bicarpellary, syncarpous; on top of the ovary is a nectar disc (stylopodium) at the base of the two stigmas; the *ovary* is bilocular with one pendulous anatropous ovule in each loculus. The **fruit** is a schizocarp (Fig. 220). Each mericarp is usually marked by five longitudinal ridges (*costae*) containing vascular bundles (3 dorsal, 2 lateral); between the ridges are furrows (*valleculae*) under which there are oil-ducts (*vittae*). Secondary ridges and vittae are frequently present between the primary ones and there are usually 2 commissural vittae. The **seed** is endospermous; the food-reserves consist of protein and oil. The embryo is small.

Pollination.—The flowers are markedly protandrous, and, the nectar secreted by the epigynous disc being easily accessible, are visited by many short-tongued insects, especially flies and beetles. The stamens are curved inwards in the flower bud, protected by the petals. They straighten and dehisce one by one, then drop off. The period over which pollen is presented to visiting insects is thus extended.

Floral formula: $K5$ or 0 $C5$ $A5$ $G(\bar{2})$.

The family is easily recognised; but, in order to distinguish with accuracy the numerous genera, careful examination of the ripe fruits is often necessary.

In India this family is best known by the cultivated plants which are commonly used as a flavouring: *Foeniculum vulgare* (saunf), fennel; *Coriandrum sativum* (dhania), coriander; *Cuminum Cyminum* (zírá), cumin seeds. *Daucus Carota* is the carrot (gájar); *Peucedanum sativum*, the parsnip; *Petroselinum sativum*, the parsley; *Apium graveolens*, the celery.

The wild Umbelliferae are mostly found in the hills, and include species of *Bupleurum*, with undivided, ovate, lanceolate or linear leaves; *Heracleum*, *Selinum*, *Chaerophyllum*, etc. A few occur at alpine altitudes, and possess a strong smell.

SUB-CLASS 2, METACHLAMYDEAE (SYMPETALAE)

O. ORDER ERICALES.—Flowers 5- to 4-merous, obdiplostemonous or the stamens opposite the petals not developed, hermaphrodite, usually actinomorphic. Petals free or usually fused. Stamens hypogynous or epigynous, rarely epipetalous carpels 2-numerous, usually equal in number to and opposite the petals, syncarpous. Ovary superior to inferior. Ovules with one integument.

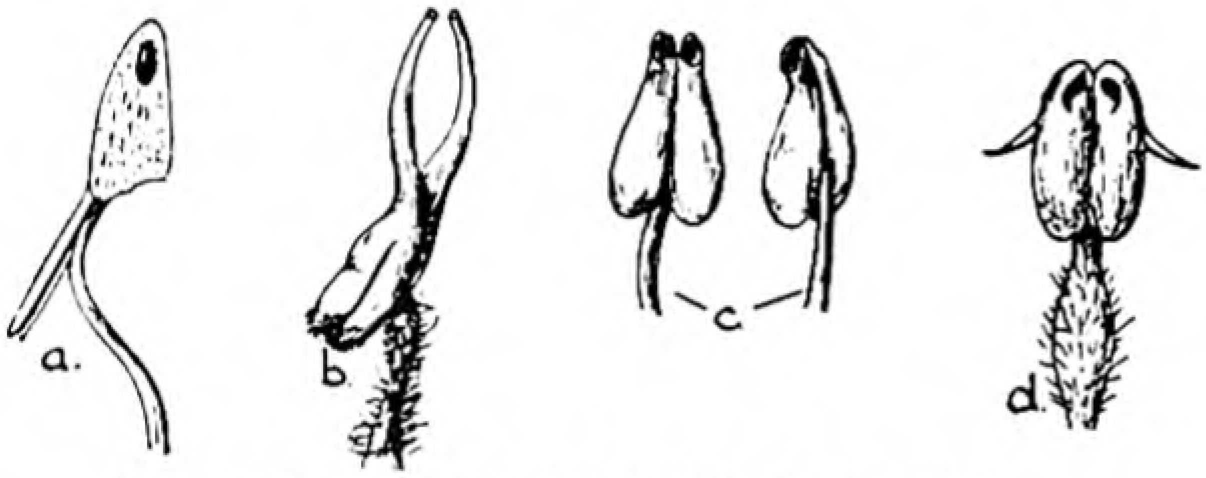

Fig. 270, A. ERICACEAE, STAMENS.
a, *Erica Tetralix*; b, *Vaccinium Vitis-idaea*; c, *Rhododendron flavum*; d, *Arctostaphylos*.

FAMILY **Ericaceae.**—Flowers 5- to 4-merous, typically obdiplostemonous, hermaphrodite. Petals rarely free, usually fused and bell-shaped and with the stamens borne round the margin of a hypogynous or epigynous disc within the calyx. Thecae of the anthers free and often spread out above. Pollen in tetrads. Ovary syncarpous, each loculus with 1-numerous anatropous or amphitropous ovules, axile placentation. Stigma capitate. Fruit a berry, drupe or capsule. Seeds with saccate testa and copious endosperm. Embryo usually very short.

This is a widely distributed family consisting of woody shrubs, often of low growth, with alternate, opposite, or verticillate, simple, exstipulate leaves. They are commonly alpine plants, or grow on moors and hills, generally in peaty soil. Many are evergreens, and more or less markedly xerophytic. The roots of most Ericaceae have mycorrhizae.

The **flowers** (Fig. 271) are usually in racemes or racemose clusters. They are bracteate, hermaphrodite, regular and actinomorphic, or slightly zygomorphic (*Rhododendron*), hypogynous or (in *Vaccinium*) epigynous. **Calyx** gamosepalous, 4- or 5-partite, persistent, inferior or (in *Vaccinium*) superior. **Corolla** regular or slightly zygomorphic (*Rhododendron*), gamopetalous, 4- or 5-fid, usually globose to broadly campanulate, imbricate in aestivation, sometimes persistent (*Erica* and *Calluna*).

Stamens eight or ten in number, rarely five (*Azalea*), obdiplostemonous, hypogynous or (in *Vaccinium*) epigynous. The anthers (Fig. 270 A) often have horn-like appendages (absent in *Rhododendron*), and open by apical slits or pores. The pollen is in tetrads (Fig. 270, B), and may be powdery (*Erica* and *Calluna*) or sticky (*Rhododendron*). **Gynaeceum** of four or five carpels, syncarpous; ovary four- or five-celled, superior or (in *Vaccinium*) inferior; ovules one to ∞ in each loculus, anatropous; placentation axile; style simple; stigma capitate or four- to five-lobed. **Fruit** a septicidal or loculicidal capsule, or a berry. **Seed** endospermous.

In the hypogynous forms there is a well-developed nectar disc at the base of the ovary (Fig. 271). The flowers are usually protandrous, and pollination is generally effected by bees, to whose visits the flowers, often pendulous, are adapted.

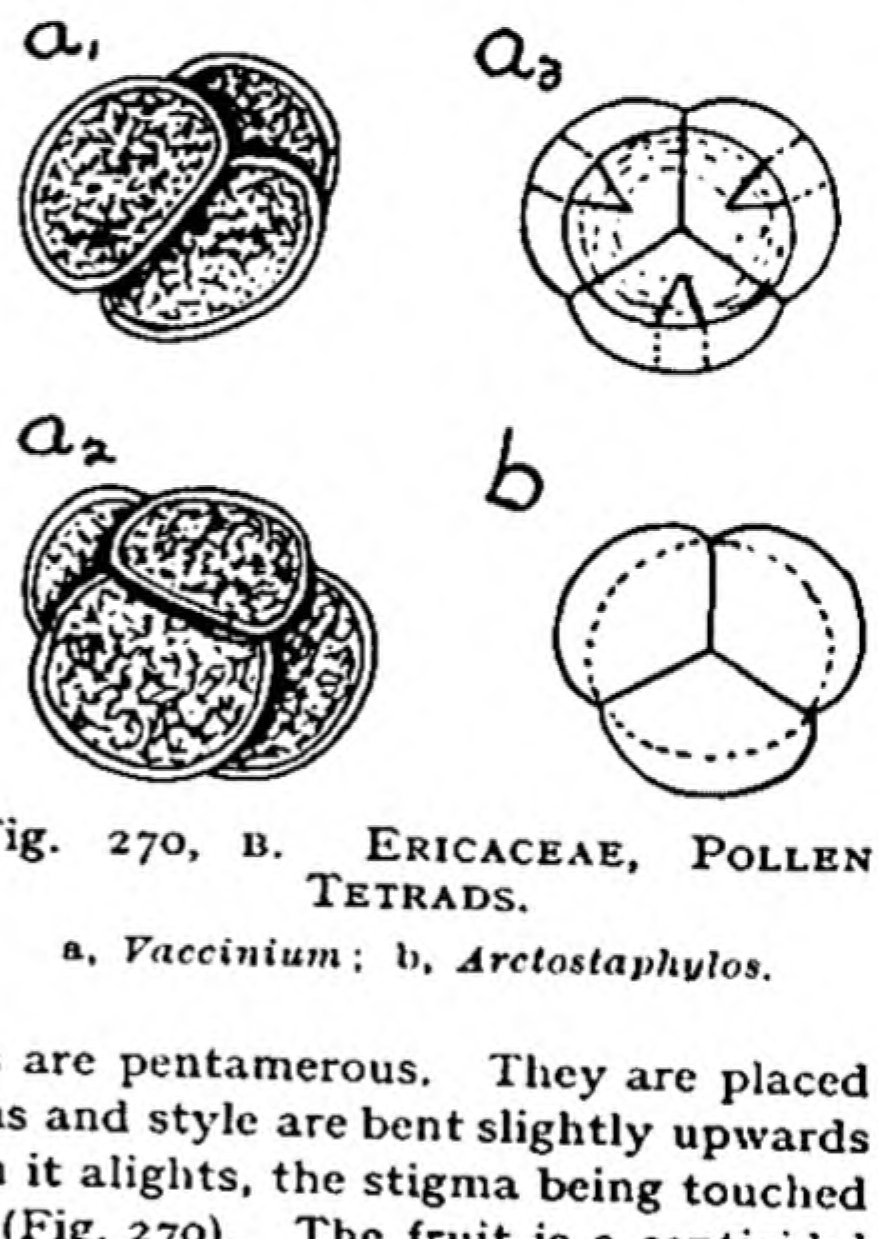

Fig. 270, B. ERICACEAE, POLLEN TETRADS.

a, *Vaccinium*; b, *Arctostaphylos*.

Rhododendron, *Vaccinium* and *Gaultheria* are the only common members of the family in India.

Rhododendron.—This genus occurs at high elevations in the hills. The leaves are usually entire, leathery, with a thick cuticle. True winter buds are generally formed. The flowers are pentamerous. They are placed more or less horizontally, and the stamens and style are bent slightly upwards so as to meet the body of the insect when it alights, the stigma being touched first. The anthers have no appendages (Fig. 270). The fruit is a septicidal capsule. *Azalea* differs from *Rhododendron* chiefly in having five stamens.

Vaccinium.—Ovary inferior, corolla usually cup- or bell-shaped (Fig. 271, B and C).

Gaultheria fragrantissima is a large shrub with white or greenish flowers in axillary racemes and blue succulent berries. The leaves yield an oil.

P. ORDER PRIMULALES.—Flowers pentamerous (rarely 4- to 8-) usually haplostemonous with antipetalous stamens, rarely also five antisepalous staminodes, hermaphrodite or unisexual, actinomorphic, rarely zygomorphic. Petals very rarely free, usually fused. Carpels invariably as many as the petals. Ovary superior or inferior, unilocular, numerous-1 ovule with two integuments on a basal or free central placenta.

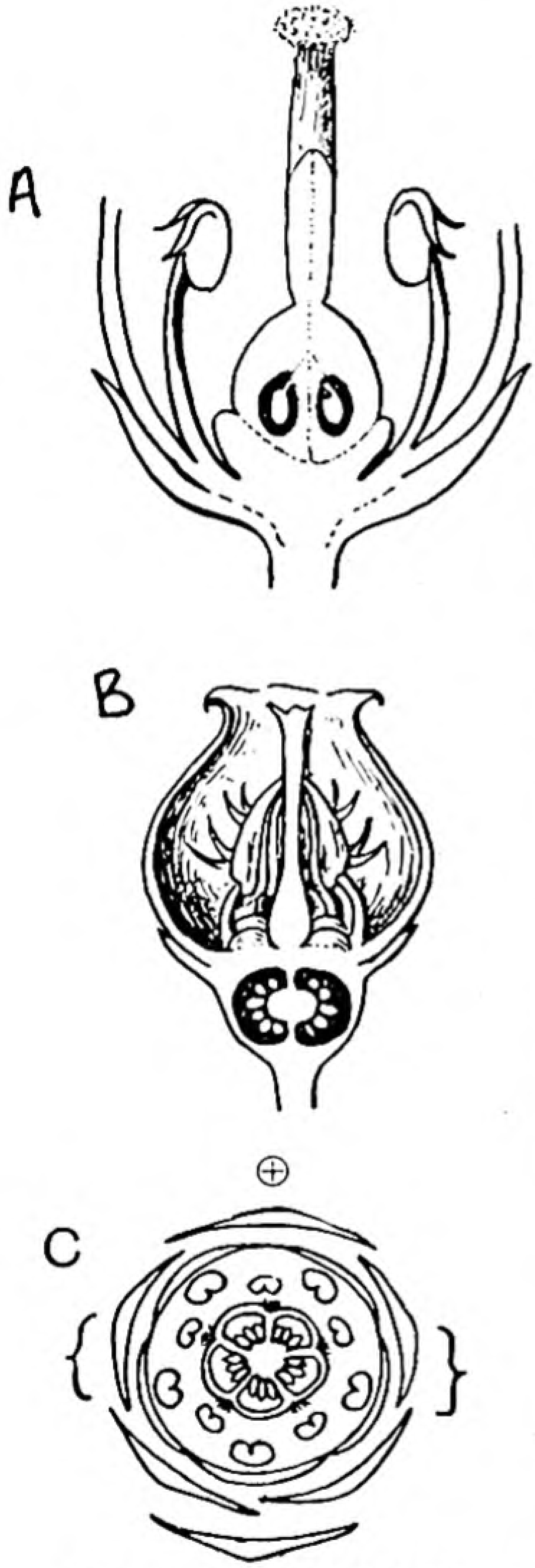

Fig. 271. ERICACEAE.
A, *Arctostaphylos*, half-flower;
B, *Vaccinium*, half-flower;
C. *Vaccinium*, floral diagram.

FAMILY **Myrsinaceae.**—Flowers in racemes, hermaphrodite or unisexual, actinomorphic. K(5) C(5) A5, antipetalous and epipetalous, outer whorl of 5 only rarely represented by staminodes. Ovary superior to inferior, unilocular, numerous ovules on a basal or free-central placenta. Stigma 1. Fruit usually a drupe or berry with one to few seeds. Embryo enclosed in a fleshy or horny endosperm.

This is a family of about 1000 species, represented in India by several genera of which *Ardisia* (Fig. 272) contains numerous species. They are mostly herbs and shrubs with alternate leaves which have no stipules, and racemes or panicles of flowers. Schizogenous resin ducts are present.

Maesa species have an inferior or semi-inferior ovary and the fruit is a small, dry or fleshy berry containing numerous seeds. They are mostly shrubs occurring in the hills.

Rapanaea consists of trees or shrubs. The ovary is superior and the fruit contains only one seed.

Embelia contains some climbing species, e.g. *E. Ribes*, which, with *E. robusta*, a shrub or small tree, provides embelia. This consists of the dried fruits which have a brittle pericarp containing a single globular seed. They resemble black pepper, but are smaller and have an astringent aromatic taste.

Ardisia consists of trees or shrubs. The fruit is a berry.

Aegiceras corniculatum occurs in the mangrove forests of the east and west coasts of India and of the Indo-Malay archipelago. The anthers split transversely and the embryos are viviparous, *i.e.* the seeds germinate whilst still in the fruits on the plant.

Q. ORDER CONTORTAE.—Flowers usually actinomorphic, pentamerous, rarely 2- to 6-merous, usually gamopetalous, rarely chori- or apo-petalous, stamens as many as petals or fewer, carpels 2, syncarpous. Stamens rarely hypogynous, usually epipetalous. Aestivation usually twisted, frequently valvate.

FAMILY **Apocynaceae.**—Flowers 5- or 4-merous, sympetalous, hermaphrodite, actinomorphic. Aestivation usually twisted, rarely valvate. Stamens 5, rarely 4, inserted in the corolla tube or at its mouth, alternating with the petals. Anthers oblong-linear or arrow-shaped, free or collected into a cone adherent to the stigma by the connective, anther lobes dehisce longitudinally, sometimes prolonged at the base into rigid spinous appendages. Carpels 2, rarely more, usually with numerous amphitropous pendulous ovules, either completely syncarpous or free below and united above by the style. Ovary in the former cases bi-locular with axile placentation. Style usually simple, thickened above into a stigmatic head which is receptive midway or at its base. Fruit a dry or fleshy drupe, berry, follicle, or samara. Endosperm slight or absent. Embryo straight, almost as long as the seed, with flat, rarely folded, cotyledons (Fig. 273).

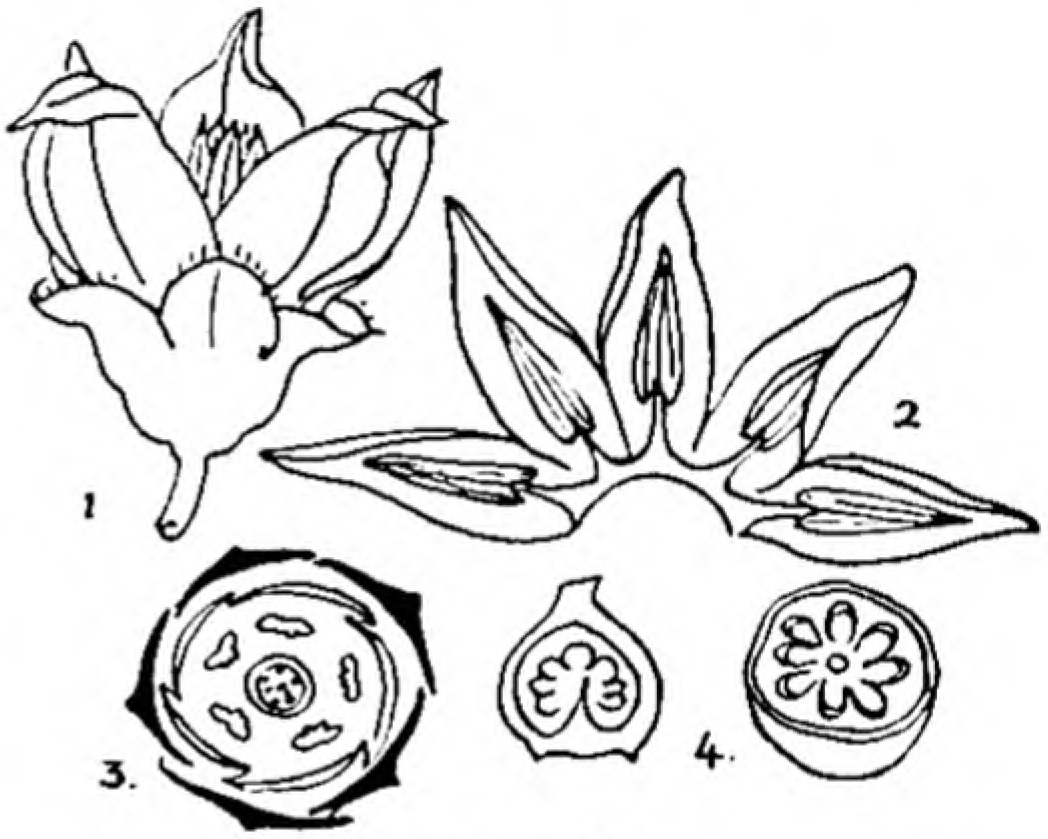

Fig. 272. *Ardisia.*

1, Flower; 2, Corolla opened out to show insertion of stamens; 3, Floral Diagram; 4, Ovary cut longitudinally and transversely.

This is a fairly large family of about 130 genera, mostly tropical and well represented in India by many common weeds as well as by plants such as the oleander and the temple tree introduced from abroad. They are trees or shrubs, erect or climbing, and also herbs. The leaves are opposite or whorled, rarely alternate, entire and without stipules. Latex cells are always present, and also perimedullary phloem.

Primarily the inflorescence is a panicle but it may ultimately show cymose branching (dichasial or a cincinnus). The fruit frequently consists of two follicles and the seeds may be provided with hairs which aid in wind dispersal (Fig. 273, A, B).

Plumeria acutifolia, the temple or pagoda tree, probably introduced from tropical America, is commonly cultivated. The flowers are very fragrant and used for garlands.

Nerium Oleander, oleander, and *N. odorum*, Indian oleander, are often cultivated as decorative plants. Other cultivated plants are *Allamanda cathartica*, a handsome climbing shrub, *Thevetia neriifolia*, both from S. America, and *Kopsia fruticosa*, a native of Burma.

Strophanthus Kombé, indigenous to tropical Africa, has seeds with long plumose awns (Fig. 273, B). The seeds contain a cardiac glycoside, strophanthin.

Alstonia scholaris, indigenous to India and the Philippine Islands, yields Dita bark, used in India for malaria, etc.

Carissa species are erect or climbing spiny shrubs. *C. Carandas* bears edible berries.

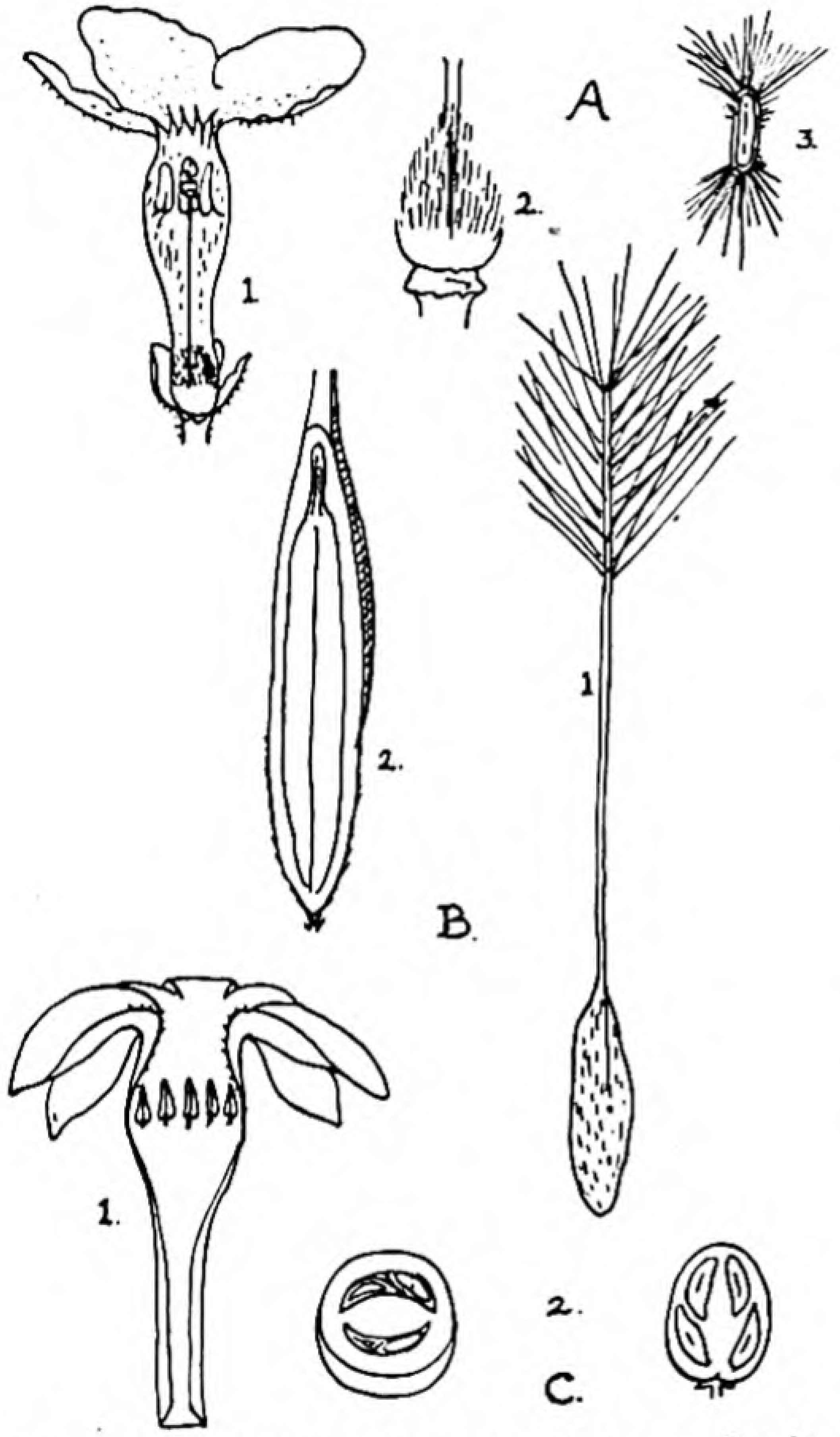

Fig. 273. *Alstonia, Strophanthus* AND *Carissa*.

A, *Alstonia scholaris*. 1, Flower in V.S.; 2, Ovary; 3, Seed.

B, *Strophanthus*. 1, Seed with plumose awn; 2, Seed in L.S. showing embryo inverted, narrow endosperm, and raphe.

C, *Carissa*. 1, Flower in V.S.; 2, Fruit cut transversely and longitudinally.

R. ORDER TUBIFLORAE.—Flowers typically with four isomerous whorls, or frequently reduced in the gynaeceum, and if zygomorphic, also with fewer stamens. Insect pollinated. Stamens epipetalous. Ovules with 1 integument.

1. FAMILY **Convolvulaceae.**—Flowers 5-4-merous, usually hermaphrodite and actinomorphic. Aestivation usually induplicate-valvate. Stamens usually epipetalous, inserted on the base of the corolla tube and alternating with the petals. Carpels (2), rarely, (3-5) superior, axile placentation, each loculus with 2 basal, erect, anatropous ovules, the micropyle facing outwards and downwards, one integument. One or two styles. Ovary on a nectar-secreting disc. Fruit a berry, nut or capsule with endospermous seeds.

Many are annuals, some are shrubs, and several are thorny xerophytes. A characteristic feature is the climbing habit, and one such genus is parasitic. Some species have tuberous roots, and latex occurs. The leaves are alternate, usually petiolate and exstipulate. The inflorescence is cymose. The calyx is imbricate and the odd sepal posterior. The corolla is bell-shaped or funnel-shaped, often plicate in the bud, usually large and brightly coloured. Extra-floral nectaries occur on the petiole of some species.

The best known genus in India is *Ipomoea*, and many species are cultivated for their attractive flowers, e.g. *I. purpurea*, known as the morning glory, *I. Learii*, *I. carnea* and *I. bona-nox*, the moon flower, whose flowers open in the evening and fade the next morning. *I. Pes-caprae* (= *I. biloba*), the goat's foot creeper, forms a characteristic feature of the flora of the sandy beaches of the eastern tropics. It has long creeping stems which root at the nodes, somewhat fleshy xerophytic leaves, and handsome purple flowers. *I. batatas*, indigenous to tropical America, is commonly cultivated for its tuberous, swollen roots, which form sweet potatoes. The little blue-flowered *Evolvulus* is common in waste places. *Convolvulus arvensis* (bindweed) is a weed of cultivation. *Cuscuta*, the dodder, is a leafless, twining parasite (p. 197). Several species occur in India.

2. FAMILY **Labiatae.**—Flowers pentamerous with reduction in the androecium and dimery in the gynaeceum, usually hermaphrodite, zygomorphic. Gamosepalous. Corolla tubular and usually two-lipped. Stamens 4, didynamous, epipetalous, or 2 stamens and 2 staminodes, or only 2 stamens. Carpels (2) each with 2 erect anatropous ovules. Fruit a tetralocular carcerulus, or, by abortion, 3-1. Seeds without or with slight endosperm. Embryo with fleshy cotyledons.

This is an important family, consisting of herbs or under-shrubs with square stems and opposite decussate, simple, exstipulate leaves. Most of them are land-plants; a few are marsh-plants. Suckers are found in many forms (Fig. 53). In most of them there are numerous epidermal glands (glandular hairs) secreting volatile oil. Well-known examples are *Plectranthus*, *Leucas*, lavender (*Lavandula*), mint (*Mentha*), ground ivy (*Glechoma*), sage (*Salvia*).

The characteristic **inflorescence** is the verticillaster (Figs. 204, 205, p. 258). The **flowers** (Fig. 274) are hermaphrodite, zygomorphic, and pentamerous, with suppression of certain parts. The **calyx** is gamosepalous, tubular, funnel-shaped, or bilabiate, persistent. The **corolla** is zygomorphic, bilabiate; sometimes, as in mint, it is almost regular. The **stamens,** owing to the suppression of the posterior one, are four in number, epipetalous and didynamous; occasionally there are only two stamens.

The **gynaeceum** is bicarpellary and syncarpous. Early in its development a median constriction appears in the ovary and produces two false septa. The style is *gynobasic, i.e.* it arises from the base and comes up from between the four parts of the ovary; this is not the case, however, in *Ajuga* and *Teucrium*. There is a bifid stigma. The ovary is quadrilocular (two true and two false septa) with one erect anatropous ovule in each loculus. The **fruit** is a carcerulus (p. 276). The **seed** is non-endospermous.

In some genera, e.g. *Thymus*, *Glechoma*, and *Prunella*, female flowers occur, usually on different plants from those with the ordinary hermaphrodite flowers. This is known as **gynodioecism.** It promotes cross-pollination.

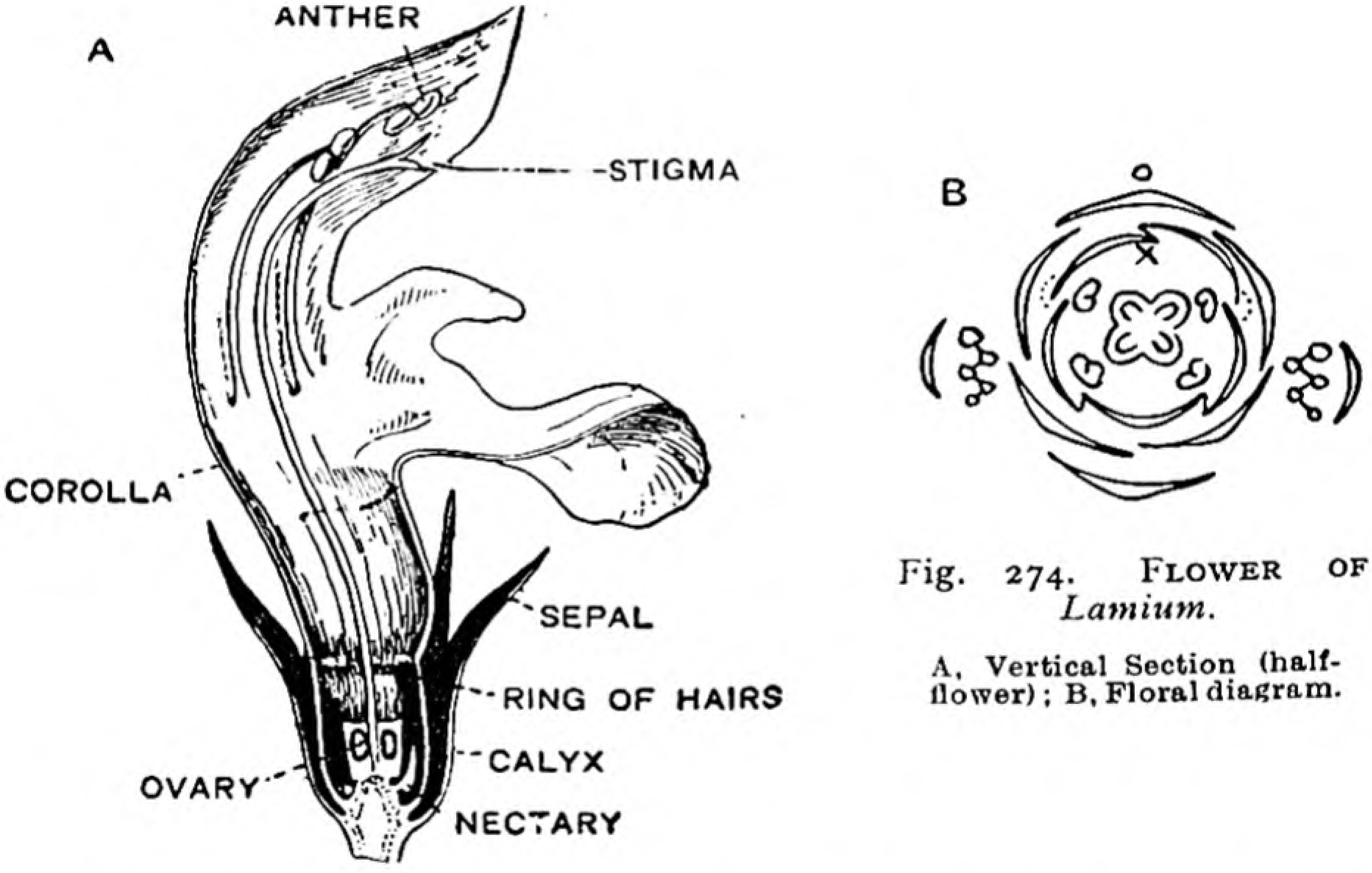

Fig. 274. FLOWER OF *Lamium*.

A, Vertical Section (half-flower); B, Floral diagram.

Pollination.—There is a nectar disc at the base of the ovary, best developed on the anterior side (Fig. 274). Usually the flowers are protandrous. In many cases, after the anthers have opened, the stamens move outwards or downwards, and the style moves into their place. When the flowers are homogamous, as in *Lamium*, the stigma projects below the anthers so as to be touched first by the visiting insect. Self-pollination, however, may take place.

In the short-tubed flowers of *Mentha*, *Thymus*, *Lycopus*, and *Origanum*, with more or less regular corolla and spreading stamens, many sorts of insects crawl over the flowers and touch the anthers and stigmas with any part of their bodies. Many Labiatae, however, are "bee-flowers" and have a conspicuous lower corolla-lip to attract insects and to act as a landing place, and usually an arched upper lip to shelter the stamens and style, which are generally placed so as to touch the bee's back as it enters the flower. Small insects may be excluded, as in *Lamium album*, by the narrowing of the lower part of the corolla-tube and the development of a ring of hairs. The mechanism in *Salvia* is described on p. 266.

This family is well represented in the Temperate Himalaya and in the plains. *Ocimum sanctum*, tulsí, sacred basil, is the most sacred of the plants of the Hindus, cultivated at their houses and temples and also used in medicine. *Plectranthus* species are numerous, some are slender herbs, others more or less fleshy herbs or undershrubs. *Coleus parviflorus* is sometimes cultivated for its edible tubers, and *C. Blumei* for its attractively coloured foliage. *C. amboinicus* is an aromatic herb used as a flavouring agent and in medicine. *Anisochilus* is a genus of herbs or undershrubs, often fleshy; *Pogostemon* of herbs, or shrubs, often aromatic; *Leucas* of pubescent herbs or shrubs, represented by many species. The genera *Lamium*, *Scutellaria*, *Prunella*, *Salvia*, *Teucrium* and *Ajuga* occur. *Salvia officinalis*, sage, is occasionally cultivated as a culinary herb,. whilst other species are grown in gardens for their showy flowers. *Mentha*, pudiná, mint is well known.

3. FAMILY **Solanaceae.**—Flowers usually 5-merous, hermaphrodite, actinomorphic or rarely zygomorphic. Corolla aestivation usually plicate-contorted. Stamens 5 (sometimes one staminodial in zygomorphic flowers). Carpels (2), obliquely bilateral, bilocular, or spuriously tetralocular, with axile placentation. Ovules numerous to one, anatropous or amphitropous, in each loculus. Fruit a berry or capsule. Endospermous seeds with straight or curved embryo.

This family is well represented in tropical countries, but only a few genera are found in Europe. It consists chiefly of herbs and shrubs with simple, more or less divided, exstipulate leaves, which are alternate in the vegetative region, but sometimes appear in pairs in the region of the inflorescence. Perimedullary phloem is present.

The following are some of the better-known members of the family: *Solanum nigrum*, the black nightshade; *S. tuberosum*, the potato; *Lycopersicum esculentum*, the tomato; *Atropa Belladonna*, the deadly nightshade; *Hyoscyamus niger*, the henbane; *Datura Stramonium*, the thorn-apple; *Nicotiana Tabacum*, the tobacco plant; *Physalis alkekengi*, the winter cherry; and the various kinds of *Petunia*, *Salpiglossis* and *Schizanthus*. *Mandragora officinalis*, the Mandrake, also belongs to this family.

Many of these plants furnish important economic products, e.g. potato, tomato, brinjal (*S. Melongena*), tobacco. *Atropa*

Belladonna, *Hyoscyamus* species, *Datura* species and *Duboisia* yield alkaloids (hyoscyamine, hyoscine, atropine) and are used in medicine. *Capsicum* species yield pungent fruits (capsicum, chillies, cayenne pepper, paprika).

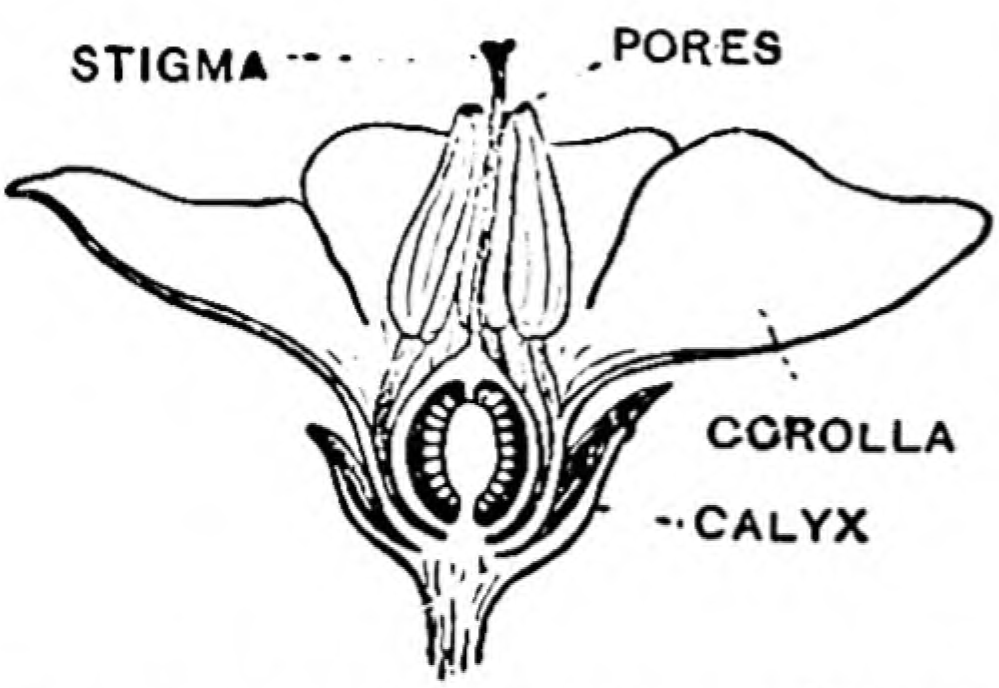

Fig. 275. Vertical Section of Flower of *Solanum tuberosum*.

The **inflorescence** is usually a cyme, in which, sometimes, the bracts are adnate to the axillary axes (see Fig. 50). The **flowers** (Figs. 275 and 276) are regular, or nearly regular, pentamerous and hermaphrodite.

The **calyx** is gamosepalous, five-cleft, and persistent; in the winter cherry, for example, it forms the red bladder-like investment to the fruit. The **corolla** is usually rotate (bitter-sweet), or campanulate (*Atropa Belladonna*). The **stamens** are five in number, epipetalous, and alternate with the lobes of the corolla. The anthers are sometimes connate (syngenesious, e.g. *Solanum*), and dehisce either by longitudinal slits (*Atropa Belladonna*) or by pores (*Solanum*).

The **gynaeceum** is bicarpellary and syncarpous; the *ovary* usually bilocular, but it sometimes becomes multilocular owing to the formation of false septa (*Datura*). The two carpels are placed obliquely in the flower and not in the median plane (Fig. 276). The **placentae** are axile, usually large and swollen, and bear numerous ovules. The *style* is single; the *stigma* simple or bilobed.

The **fruit** is a capsule (*Hyoscyamus* and *Datura*) or berry (*Solanum* and *Atropa*). The **seed** is endospermous. The embryo is frequently characteristically curved (Fig. 277). The flowers are entomophilous. *Nicotiana* is pollinated in the evening by moths. *Solanum* is visited for pollen; no nectar is secreted.

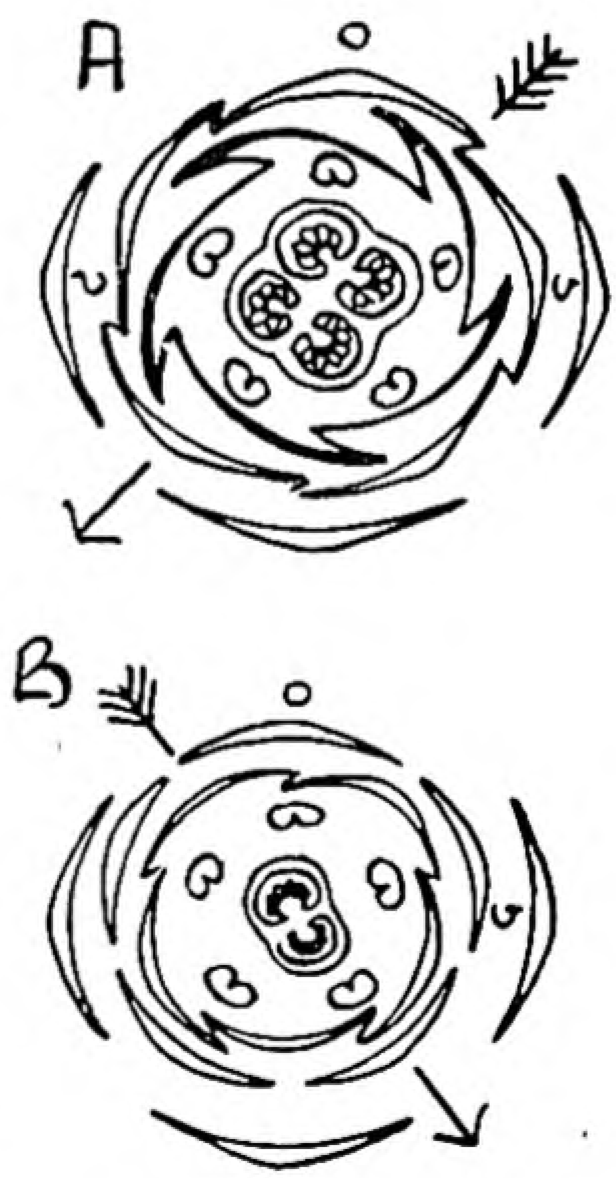

Fig. 276.

A. Floral Diagram of *Datura Stramonium*; B, Floral Diagram of *Hyoscyamus albus*.

The Solanaceae are closely allied to the Scrophulariaceae. They are distinguished from the latter by their regular or nearly regular flowers, and by the oblique position of the carpels (a character, however, not easily recognised).

Typical floral formula: $K(5)\ \widehat{C(5)\ A5}\ \underline{G(2)}$.

These numbers may be modified in cultivated plants. Thus in cultivated tomato the flowers may be hexamerous and the ovary multilocular.

Solanum is represented in India by numerous wild species. The potato is largely cultivated in the hills. *Physalis peruviana*, the Cape gooseberry, introduced from S. America, is cultivated and runs wild. *Datura fastuosa* and its var. *alba* are apparently wild. *D. Metel* and *D. Stramonium*, thorn apple, also occur in some districts, and other species, e.g. *D. suaveolens*, trumpet flower, are cultivated. The tomato is commonly cultivated. *Capsicum annuum* and *C. frutescens*, both introduced originally from S. America, are extensively cultivated as chillies. Tobacco is cultivated in many districts. *Hyoscyamus niger*, henbane, and *Atropa Belladonna*, deadly nightshade, grow wild in the N.W. Himalaya.

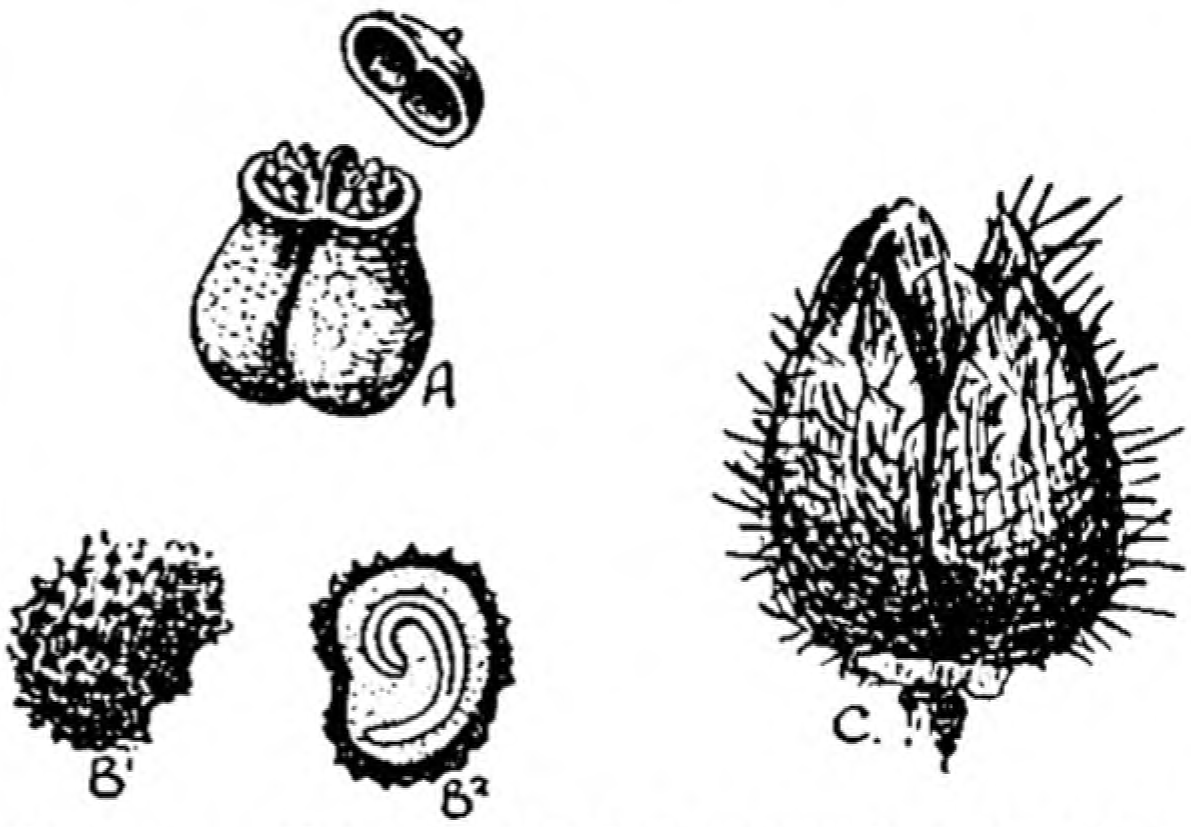

Fig. 277. FRUITS AND SEEDS OF SOLANACEAE.

A, *Hyoscyamus niger*, fruit; B, *Hyoscyamus niger*, seed, (1) entire, (2) in longitudinal section; C, *Datura Stramonium*, fruit.

4. **FAMILY Scrophulariaceae.**—Flowers 5-merous, hermaphrodite, more or less zygomorphic. Stamens rarely 5, usually 4 or 2. Carpels (2), median, ovary bilocular, each with numerous to few anatropous or amphitropous ovules. Placentation axile. Fruit a capsule, or berry. Embryo straight or feebly curved in endosperm.

This family is readily distinguished from Labiatae by its fruit. Most of the plants belonging to it are herbs or under-shrubs, with alternate or opposite, exstipulate leaves. Some are climbers, e.g. *Maurandia*, which has sensitive petioles, a native of Mexico but naturalised in some districts. The stems are usually cylindrical. Foxglove (*Digitalis*), speedwell (*Veronica*), snapdragon (*Antirrhinum*), toadflax (*Linaria*), and *Calceolaria* are members of this family.

The family includes a number of semi-parasites: e.g. *Striga* and *Pedicularis* (see p. 198).

There are various forms of **inflorescence.** Racemes and spikes are common, but sometimes the lateral branches are cymose; occasionally the flowers are solitary and axillary. Bracts and bracteoles are generally present. The **flowers** (Fig. 278) are hermaphrodite, zygomorphic; they are typically pentamerous, but there are various modifications due to suppression and fusion.

The **calyx** is gamosepalous, usually 5-lobed, persistent; in *Veronica* and *Calceolaria* the posterior sepal is suppressed. The **corolla** is gamopetalous, usually two-lipped, hypogynous; in the mullein (*Verbascum*) it is nearly regular; in *Antirrhinum* and *Linaria* it is bilabiate and personate; in foxglove it is glove-shaped; in *Veronica* rotate, and 4-lobed owing to the fusion of the posterior pair of petals; in *Linaria* it is spurred.

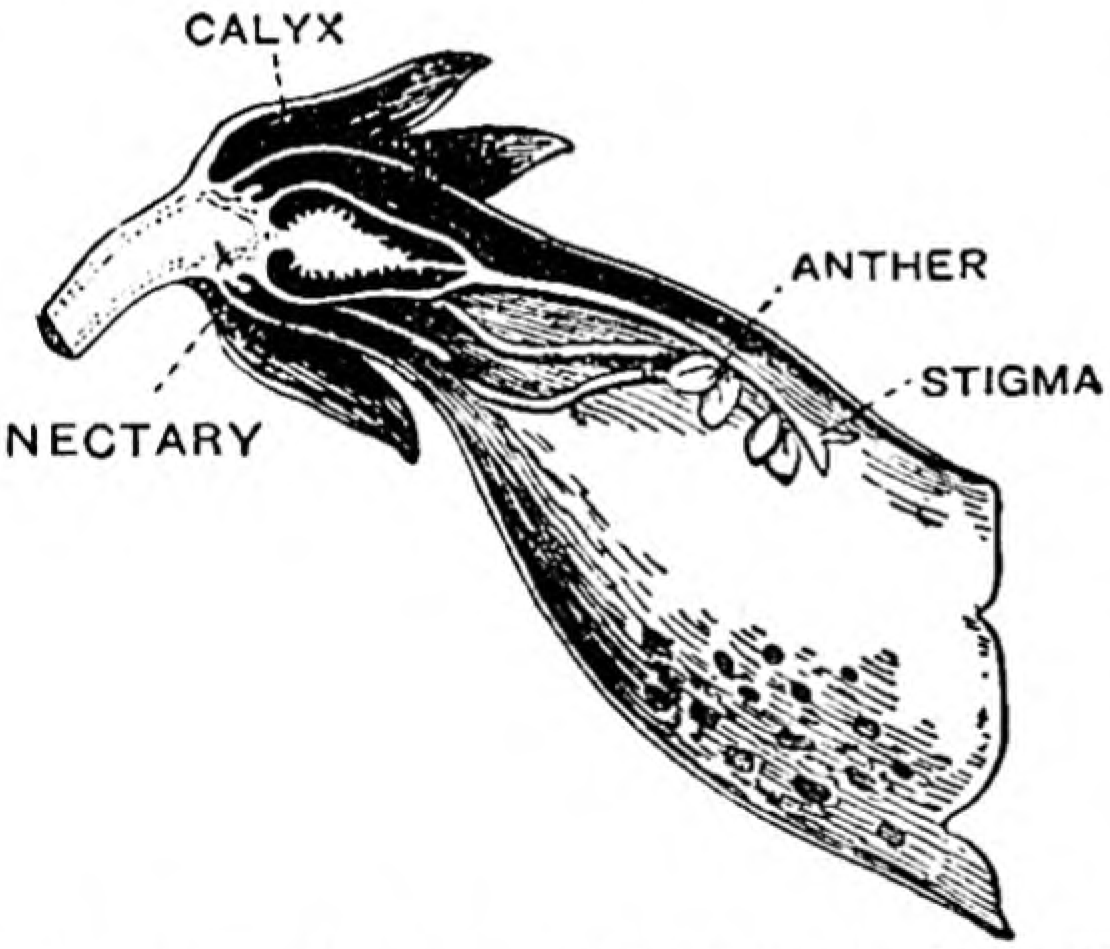

Fig. 278. Vertical Section of Flower of *Digitalis*.

The **stamens** are usually 4 in number, epipetalous, didynamous. The posterior stamen has been lost; it is present, however, in the mullein (*Verbascum*), and is represented by a staminode in the figwort (*Scrophularia*) and *Pentstemon*. In *Veronica* and *Calceolaria* there are only 2 stamens, the anterior pair also having been suppressed. The **gynaeceum** is bicarpellary, syncarpous; the style single, the stigma entire or 2-lobed. The carpels are in the median plane (see Fig. 194). The ovary is bilocular, superior. The anatropous ovules are usually numerous, and borne on a large, axile, dumb-bell-shaped placenta. The **fruit** is a capsule, dehiscing loculicidally or by pores. The seeds are usually numerous and endospermous.

Floral formulae: *Digitalis*—$\mathrm{K}(5)\ \overparen{\mathrm{C}(5)\ \mathrm{A}4}\ \mathrm{G}(\underline{2})$.

Veronica—$\mathrm{K}(4)\ \overparen{\mathrm{C}(4)\ \mathrm{A}2}\ \mathrm{G}(\underline{2})$.

Pollination.—There is a nectar disc at the base of the ovary. The flowers as a rule are only slightly protandrous, and in most cases self-pollination may occur; but the stigma usually protrudes beyond the stamens and so is touched first by the visiting insect. Open flowers like those of speedwell and mullein are mostly pollinated by hover-flies. In speedwell the stigma bends down over the large lower petal, while the two stamens project over the lateral petals. The insect first touches the stigma and then, in seeking for the nectar, which is protected by a ring of hairs, seizes the stamens and tucks them under its body, thus getting dusted with pollen. Many of the smaller-flowered species of *Veronica* are self-pollinated.

Most of the flowers, however, are pollinated by bees—those with closed (personate) corollas by humble-bees. The flowers of the semi-parasitic species are known as "loose-pollen flowers." The pollen is dry, and the anthers are protected by the well-developed upper corolla lip. The anthers are joined by hairs to form a "pollen-box" in which the pollen collects. The insect on entering the flower shakes the anthers, and gets dusted with pollen.

The flowers of figwort (*Scrophularia*) are protogynous and pollinated by wasps.

Indian species of *Verbascum* are woolly mullein (*V. Thapsus*), introduced from Europe, with dense covering of woolly hairs, yellow corolla; and *V. virgatum*, also introduced and naturalised at high levels. Floral formula: $\mathrm{K}(5)\ \overgroup{\mathrm{C}(5)\ \mathrm{A}5}\ \mathrm{G}(\underline{2})$. *Linaria ramosissima*, a toadflax, with small yellow, spurred flowers, is a perennial prostrate herb, growing on walls and rocks.

Antirrhinum orontium is the corn snapdragon. It is an annual growing in cornfields, etc. *A. majus*, snapdragon, grows on old walls, rubbish heaps, etc. Both occur in hilly districts. *Scrophularia peregrina*, a native of Asia Minor, occurs as a roadside weed, e.g. in the Nilgiris. The foxglove (*Digitalis purpurea*) is a biennial cultivated for its leaves which contain valuable medicinal substances.

There are several annual species of *Veronica*, e.g. *V. agrestis* (procumbent or green field speedwell), in waste places and cultivated soil; *V. persica*, in fields and cultivated soil, both with solitary axillary flowers. *V. arvensis* (wall speedwell), with two opposite lines of hairs on the stem, found in dry, sandy places, and *V. javanica*, pubescent, with much branched, slender stems, have the flowers in terminal racemes.

Pedicularis species are root parasites found in grasslands at high elevations: *Striga* species similarly attack cultivated Sorghums.

Calceolaria chelidonioides (with inflated, "slipper-shaped" yellow corolla), is a weed from Mexico now naturalised in the hills. In *Mimulus* the stigma-lobes are flat and sensitive to contact, closing up when touched; self-pollination is thus prevented as the insect leaves the flower.

Celsia coromandeliana, with an almost regular corolla, grows in the plains and the lower hills of India. *Torenia Fournieri*, introduced from Cochin China, is a popular garden plant; several other species grow wild. *Limnophila* species are marsh or water plants, generally aromatic.

5. FAMILY **Acanthaceae.**—Flowers 4-5-merous, usually hermaphrodite, zygomorphic. Calyx free or fused, corolla generally strongly two-lipped; stamens 4 or 2, frequently also 1-3 staminodes, one anther-lobe may be smaller than the other or completely abortive, the pollen shows a variety of patterns which are generally constant for the genus and useful in classification. Carpels (2), median, each loculus with numerous to 2 ovules, anatropous or amphitropous, arranged in 2 rows or 1. Style long, with 2 stigmas of which the posterior one may be the smaller. Fruit usually a bilocular capsule, loculicidal to the base, stalked, with non-endospermous seeds; rarely a drupe.

This is a very large family, well represented in India by many common plants, which show a great variety of habit, some being climbers, some xerophytes, some shore plants. Mostly they are herbs or shrubs, with opposite exstipulate leaves, which are usually entire. Perimedullary phloem is frequently present and cystoliths occur.

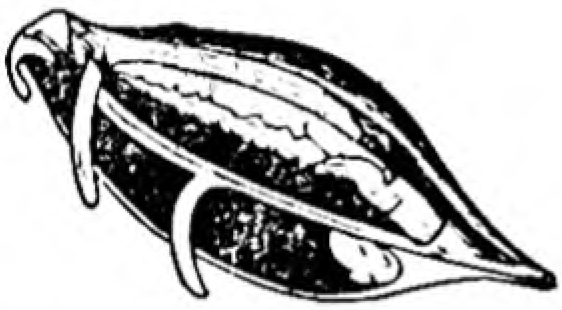

Fig. 279. HALF OF FRUIT OF *Acanthus mollis*, SHOWING JACULATORS.

The **inflorescence** is a dichasial cyme with a tendency to become monochasial in the later branchings, and quite frequently the cyme is "condensed" in the axils of the leaves in such a way as to appear like a small whorl of flowers, whose cymose nature can be recognised by the fact that the central flowers open first. These cymes develop in racemose order, and actual racemose inflorescences also occur. The **bracts** and bracteoles are often large and coloured, the latter sometimes enclosing the flower and performing to a greater or less extent the functions of a calyx.

In most of the family the seeds have peculiar outgrowths (*jaculators*) from the stalks, which are sometimes of hook-like, sometimes of papillar shape (Fig. 279). These lignify and stiffen, and by bending into a more or less horizontal position press the fruit walls outwards until it bursts with a jerk and throws out the seeds. In *Ruellia* and others the seeds have hairs upon the surface which swell up when wetted and may be of use in anchoring the seed to its place of germination.

The flower secretes nectar by a disc below the ovary, and by its size and complication is usually adapted to the visits of bees, while its pollination mechanism is perhaps most commonly that which has been described under Scrophulariaceae as the loose-pollen mechanism.

Among the more common members of the family are *Thunbergia*, a climbing (twining) plant with a much divided calyx, *Ruellia*, mentioned above, *Barleria*, *Justicia*, *Adhatoda*, and other common weeds. *Acanthus ilicifolius*, with its pretty flowers and prickly leaves, is common among the mangrove and swamp formations upon the coasts. But perhaps the most interesting genus of the family is *Strobilanthes* (Fig. 280), of which numerous species grow in the forests upon the hills, and form a characteristic feature of the mountain flora, though a few species are occasionally found at low levels. These plants form the undergrowth of the forests where they occur. They grow without flowering for several years, and then all flower simultaneously, the forest being then for a short time a sea of flowers, with innumerable bees at work among them; later the seeds are ripening, and the forest is full of jungle fowl feeding upon them; and finally there is nothing but a wilderness of dead shoots, until the young plants begin to appear and repeat the same history. Every mountain range, especially in the south, has numerous species of *Strobilanthes* confined to it, that is, endemic there.

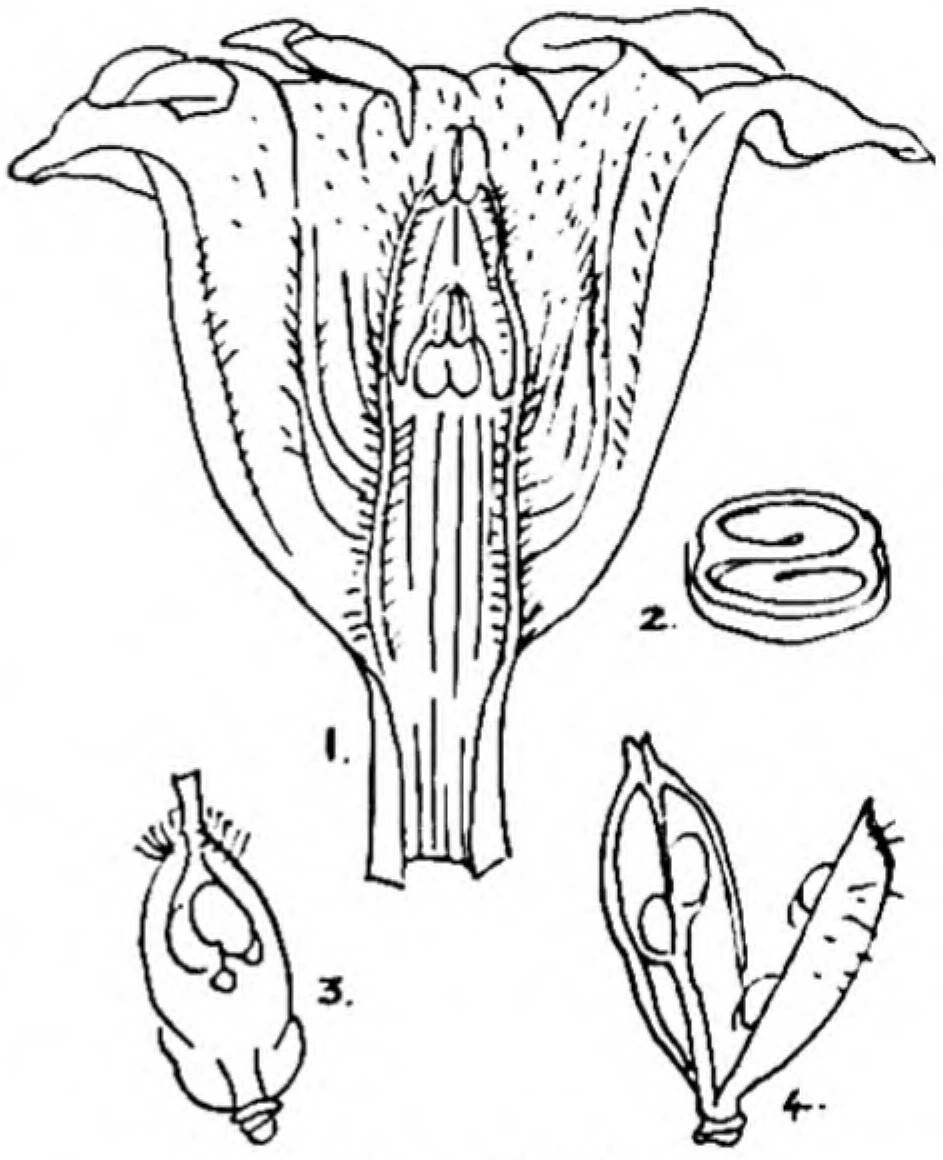

Fig. 280. *Strobilanthes*.

1. Corolla opened out showing the two stamens; 2 and 3. Ovary cut transversely and longitudinally; 4. Fruit opened loculicidally.

S. ORDER RUBIALES.—Flowers typically 5- to 4-merous, with as many or fewer stamens and carpels, actinomorphic, rarely zygomorphic or irregular. Ovary inferior, as many loculi as carpels but most usually bilocular, each loculus with numerous to 1 anatropous ovules with 1 integument.

FAMILY **Rubiaceae.**—Flowers 5- to 4-merous, rarely more, with isomerous or usually oligomerous inferior ovary. Hermaphrodite, rarely unisexual, actinomorphic, rarely zygomorphic. Calyx usually insignificant, sometimes, as in *Mussaenda*, one of the sepals is large and brightly coloured, forming the most conspicuous part of the flower and serving to attract insects. Corolla aestivation valvate, convolute or imbricate. Carpels usually (2), rarely 1-(∞), each loculus with ∞-1 anatropous ovules. Style simple, stigma capitate or lobed. Fruit most commonly a capsule, often a berry, less frequently a schizocarp. Seeds rich in endosperm, embryo small. Inflorescence cymose, usually much branched, frequently in small dichasia.

This is one of the largest families of tropical plants, and represented in India by many native and cultivated plants; they are mostly trees and shrubs, but there are also a considerable number of herbs. The **leaves** are entire or very rarely toothed, and are always stipulate. The **stipules** show great variety in form. Only comparatively rarely are there two stipules to a leaf, standing one on either side of it. Sometimes they are united in pairs, one of one leaf to the one of the other standing beside it (interpetiolar); sometimes they are united between the petiole and the stem (intrapetiolar); sometimes they are united to one another and to the leafstalks, so as to form a sheath round the stem. In the tribe Galieae, to which belong the genera *Galium* and *Rubia*, the stipules are large and leafy, resembling the leaves, except that they have no axillary buds. Sometimes they are united in pairs, so that, with the two leaves, a whorl of four is formed, sometimes free, forming with the leaves a whorl of six.

The family is divided into two sub-families according to whether the ovary contains numerous ovules in each loculus (Cinchonoideae) or only one (Coffeoideae).

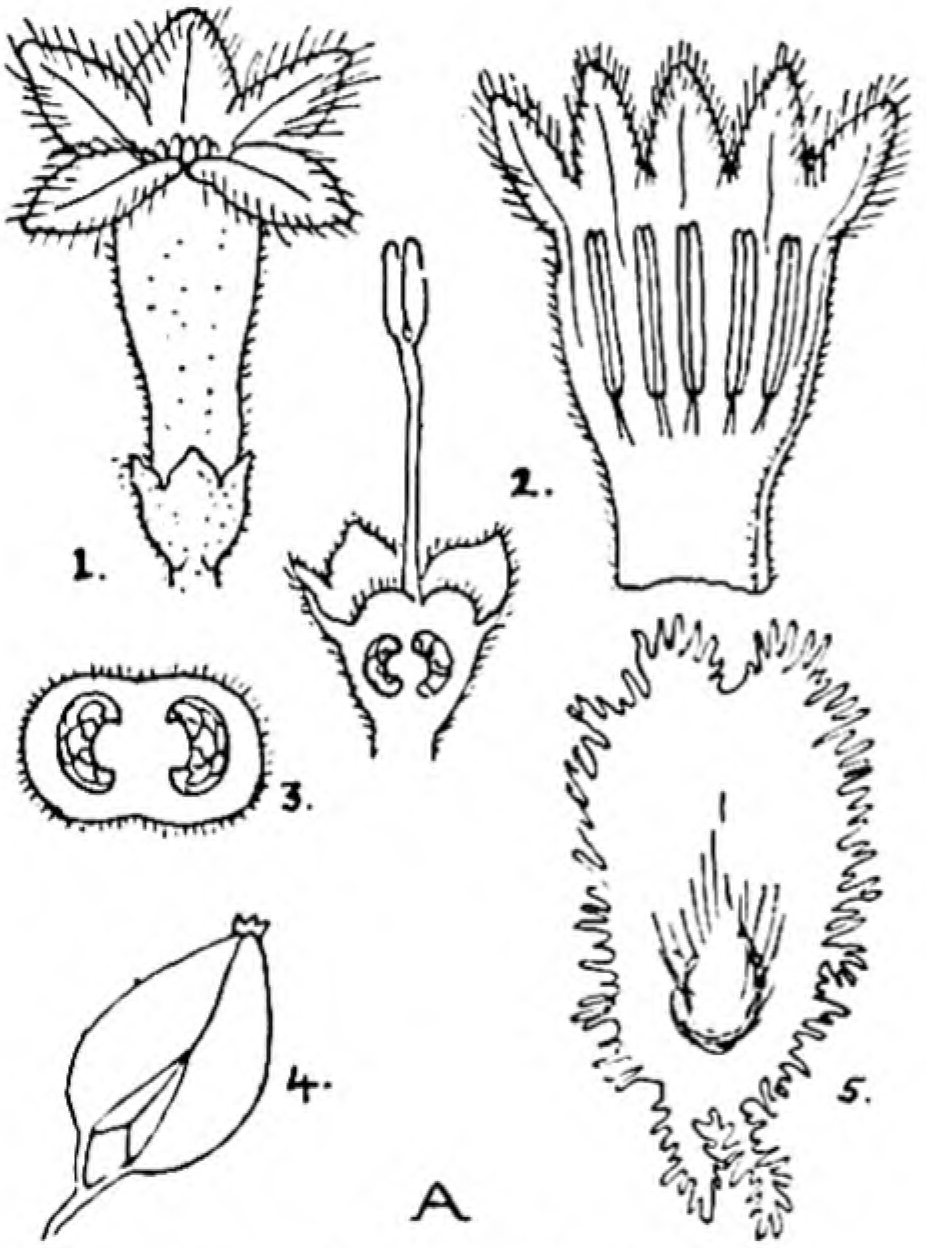

Fig. 281, A. *Cinchona*.

1, Flower; 2, Corolla opened out showing insertion of stamens; 3, Ovary in T.S. and L.S.; 4, Fruit, splitting from below; 5, Seed (enlarged).

Among the more interesting members of the family to be found in India are the following:—

I. **Cinchonoideae.**—*Oldenlandia* (including *Hedyotis*), a number of species of which are common weeds, especially on the seashore, and one of which, *O. umbellata*, the chay-root, affords a dull pinkish purple dye from its roots, formerly much employed in India for dying cloths; another species of interest is *O. verticillaris* of the Nilgiris and Ceylon, with a kind of basin formed by the broad expanded bases of the leaves, in which a considerable amount of water is collected and held; *Cinchona*, the source of the quinine and cinchonidine of commerce, originally a native of Peru, was introduced into Java by the Dutch in 1852, brought to India and Ceylon in 1861 by Sir Clements Markham, and now extensively cultivated, e.g. in the Nilgiris and about Darjiling; *Gardenia*, many species of which are native or cultivated in India; *Nauclea Cadamba* (= *Anthocephalus indicus*), the kadam tree, cultivated for ornament.

II. **Coffeoideae.**—*Knoxia*, a common weed in the hills of the south, shows heterostyly; *Coffea*, some species of which are native in India, but *C. arabica*, Arabian coffee, and *C. liberica*, Liberian coffee, are largely cultivated; *Ixora*, many species of which are to be found, some of them with very showy and handsome flowers, with long tubes preventing the nectar being obtained by any but Lepidopterous insects; *Pavetta*, a shrubby genus, of which several species occur, and which are marked by the presence of little pustules on the leaves, inhabited by colonies of Bacteria. *Morinda*, some species of which are found on the seashore and others in the hills, which have the flowers densely aggregated, with a certain amount of union of calyces, etc., while the fruits are combined by the succulent enlarged calyces into one dense compound fruit.

Species of *Galium* and *Rubia* occur. The roots of *R. cordifolia*, Indian madder, yield the red dye known as Manji't.

Other plants of interest in this family are *Uncaria gambier*, Indo-Malay, yielding catechu, used medicinally; *Cephaëlis Ipecacuanha*, Brazil, the source of ipecacuanha root containing valuable alkaloids; and the myrmecophilous *Hydnophytum* and *Myrmecodia*, both of Indo-Malay, epiphytes possessing tubers inhabited by ants.

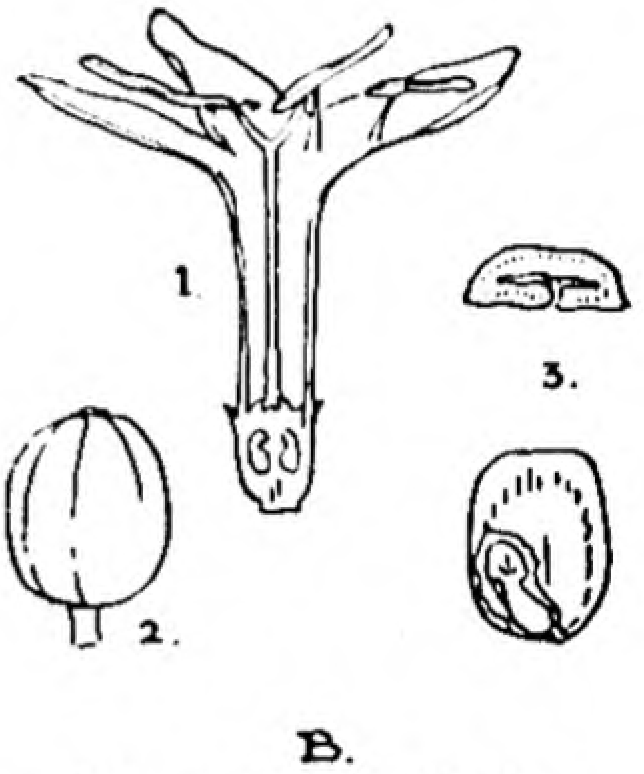

Fig. 281, B. *Coffea*.
1. Flower in V.S.; 2. Fruit; 3. Seed in T.S. and L.S.

T. ORDER CUCURBITALES.—Flowers typically 5-merous. Anthers with 2 unilocular thecae, either 5 free, or 4 fused in 2 pairs, or all five united into a central column. Carpels usually (3) with axile placentation, rarely 1-(10), inferior, the 2 placentae extending deeply into each loculus and bending backwards near the wall of the ovary, usually ∞ anatropous ovules per loculus, rarely few to one. Stigmas as many as the carpels.

FAMILY **Cucurbitaceae.**—Flowers rarely hermaphrodite, usually unisexual, actinomorphic. Receptacle cup-shaped. Style 1 with 3 usually forked stigmas. Fruit usually a berry. Seeds non-endospermous. Embryo with large, broad, cotyledons storing oil.

This is a fairly large family, well represented in India by plants which are mostly climbing annuals, which grow rapidly and climb by aid of tendrils. The morphological nature of these has been in question, but the view which perhaps finds most favour is that the tendril is of dual nature, the lower part being stem, the upper leaf. The tendrils exhibit nutation and are sensitive to contact with solid objects. The leaves are alternate, often palmately notched. The vascular bundles are bicollateral (Fig. 68).

The **inflorescence** is of various types. The **stamens** are typically 5, but there is great variety in the androecium, which is usually zygomorphic, and has cohesions of various types. The anthers are always 2- not 4-locular. Only very rarely are there 5 stamens present, each with a bilocular anther. In most of the family there appear to be 3 stamens, two of which have 4-locular anthers; in reality this is due to a fusion of two pairs of stamens, leaving the fifth free. At the same time the anther loculi usually become much curved, and in some the pollen-sacs are remarkably twisted (Figs. 282, A, and 282, C).

The **fruit** is usually fleshy, of the type exhibited in the pumpkin or the cucumber—a berry-like fruit sometimes called a pepo, with exalbuminous seeds.

Many of the family are cultivated for their fruits, e.g. *Trichosanthes Anguina*, the snake gourd; *Momordica Charantia*, the karéla; *Lagenaria vulgaris*, the bottle gourd (kaddu); *Citrullus vulgaris*, the water melon, an African species; *C. Colocynthis*, the colocynth or bitter gourd, used in medicine; *Cucumis sativus*, the cucumber; *C. Melo*, the melon; *Benincasa cerifera*, the ash pumpkin or white gourd melon, whose seeds yield an oil; *Cucurbita maxima*, the squash-gourd or pumpkin; *C. Pepo*, the pumpkin; *C. ovifera*, the vegetable marrow; and *C. moschata*, the musk melon; *Luffa aegyptiaca*, the loofah or bath sponge, whose fruit contains a network of vascular bundles, which when set free by the rotting away of the softer tissue forms an excellent bath sponge; and many others of less interest.

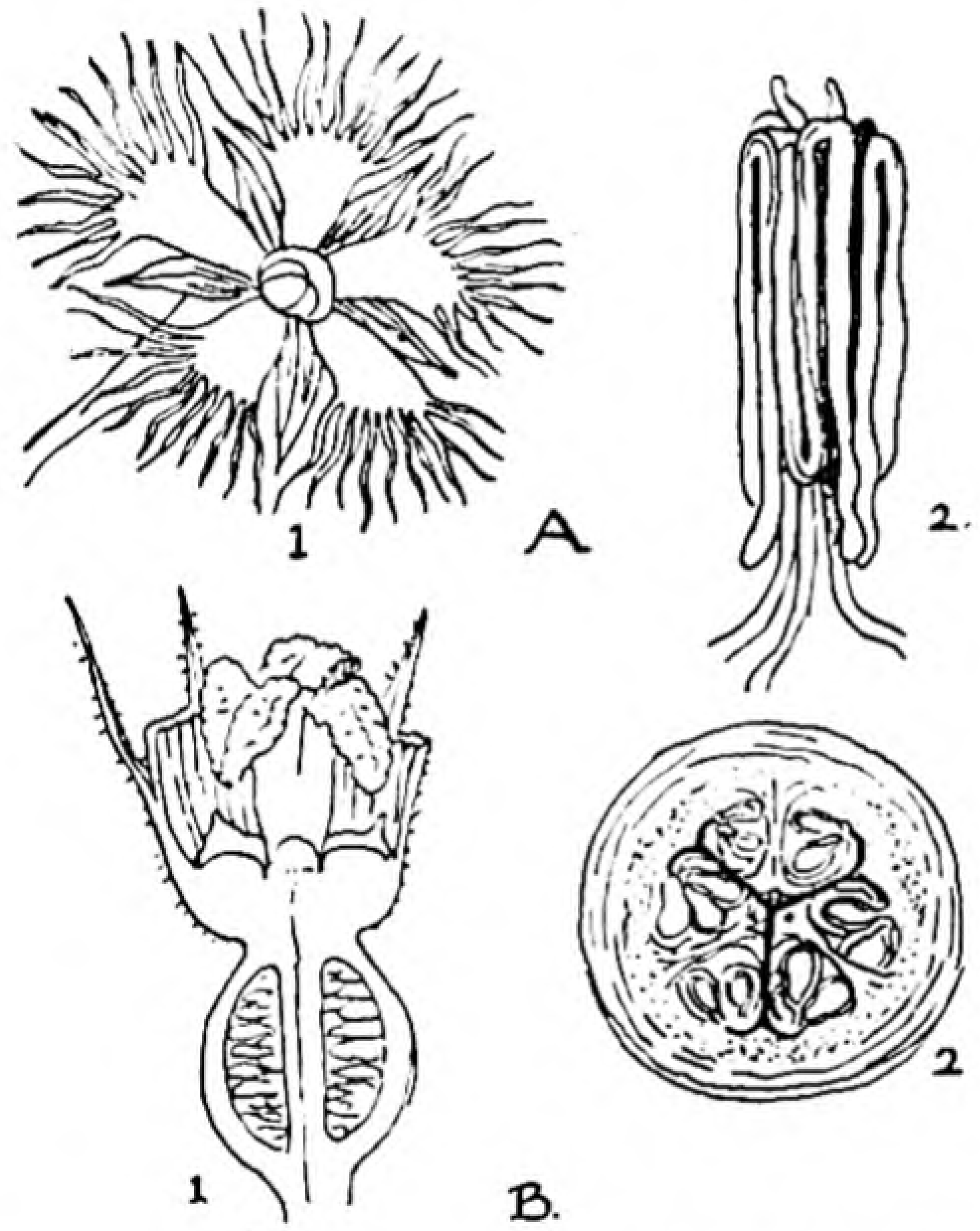

Fig. 282. *Trichosanthes* AND *Cucurbita*.

A, *Trichosanthes palmata*; 1, Upper part of female flower; 2, Group of stamens from male flower. B, *Cucurbita Pepo*; 1, V.S. lower part of female flower; 2, T.S. Ovary.

U. ORDER CAMPANULATAE.—Flowers typically pentamerous except perhaps the ovary. Anthers with bilocular thecae, completely or partially syngenesious. Ovary inferior, multilocular each with numerous to one ovule, or unilocular with one ovule.

FAMILY **Compositae.**—Flowers 5-merous, hermaphrodite, unisexual or neuter, actino- or zygo-morphic. Calyx rarely clearly developed, usually represented by a ring of small teeth or numerous hairs, bristles or scales, the so-called pappus. Corolla two-lipped or strap-shaped (ligulate) or tubular (Figs. 177, C, and 283). Stamens epipetalous, with free filaments and syngenesious anthers, introrse dehiscence. Carpels (2), median; inferior ovary unilocular with one basal anatropous erect ovule. Style forked at the tip in the fertile flowers, the upper (inner) surfaces receptive, and provided with a brush mechanism. Fruits one-seeded cypselas.

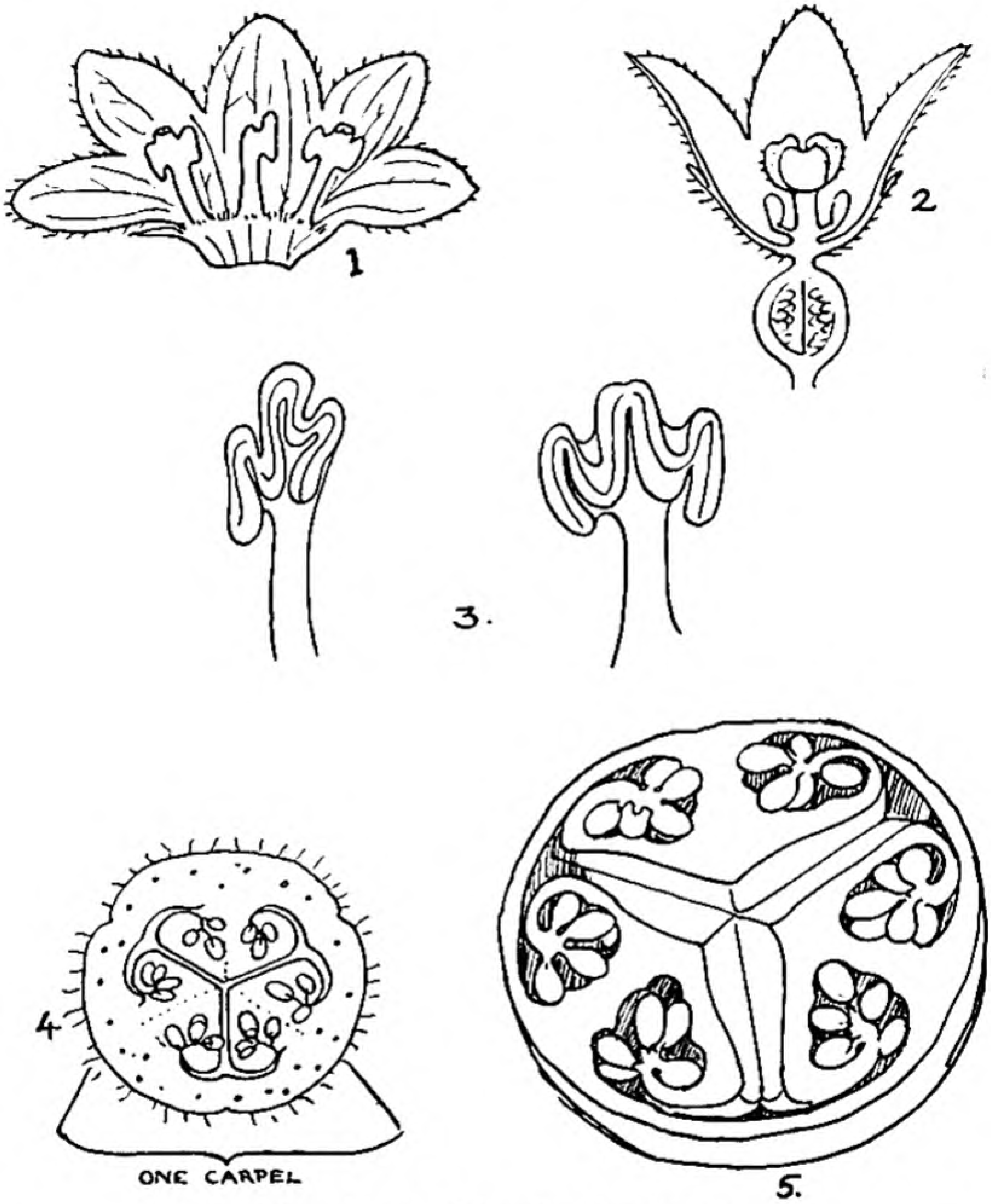

Fig. 282, c. *Citrullus Colocynthis.*

1, Male flower, corolla opened out; 2, Female flower, V.S.; 3, Smaller and larger stamen; 4, Ovary, T.S., semi-diagrammatic; 5, Fruit, T.S.

Seeds non-endospermous. Embryo straight. Characteristic inflorescence (capitulum).

This is the largest and most widely distributed family of flowering plants, including about 14,000 species. The plants are nearly all herbaceous; only in certain parts of the globe is the order represented by shrubs (e.g. *Vernonia* spp.). They present great variety in their vegetative organs, as would be expected, considering they are found in very diverse situations, but water-plants, climbing plants, and epiphytes (p. 153) are not common in the order. There is usually a tap-root, often more or less thickened, e.g. dandelion and *Elephantopus*. The leaves are usually radical, or alternate, less frequently opposite (sunflower, *Siegesbeckia*, *Dahlia*), usually exstipulate. Laticiferous vessels are found in the Liguliflorae, and oil-ducts are common in the family. Frequently perimedullary phloem is present, and inulin occurs as a reserve food-material.

The inflorescence is with few exceptions a capitulum, containing numerous small flowers (florets) surrounded and protected by an involucre (Fig. 201). The disc is usually flattened or convex. The flowers in the capitulum may be all ligulate or all tubular or the outer may be ligulate and the inner tubular. The youngest are in the centre. Small scaly bracts, called **paleae,** are frequently present between the flowers (e.g. sunflower), and the capitulum is then described as *paleaceous*. Sometimes hairs or bristles take the place of scales (e.g. in thistles). The capitula may be arranged in racemes, panicles, spikes, etc. The pappus, when present, may be sessile on the ovary, or may after fertilisation be carried up on a stalk (Fig. 214, A).

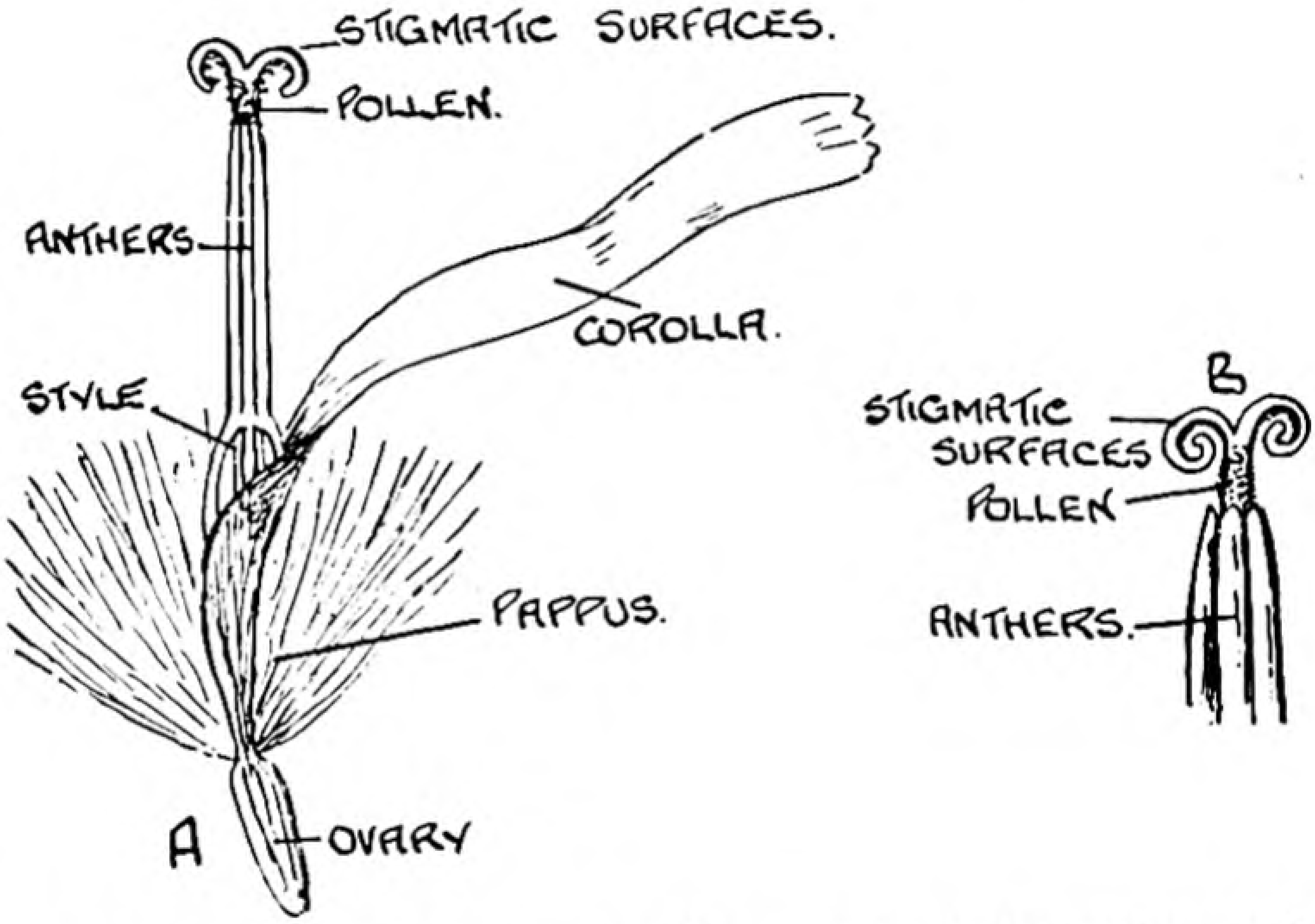

Fig. 283. Compositae, Pollination Mechanism in *Hieracium umbellatum.*

The mechanism of **pollination** is interesting. The flowers are protandrous. The pollen is shed into the tube formed by the anthers. The style and stigma elongate through this tube and *gradually* brush out the pollen, which is carried away in large quantity by insects visiting the capitulum. The stigmas do not unfold till they have grown out of the anther tube; and, as only the upper surface of the stigma is receptive, self-pollination is prevented at this stage. If cross-pollination does not take place, self-pollination may be effected later by the stigmatic lobes bending back and reaching any pollen remaining on the hairs (Fig. 283).

The corolla tube is usually short enough to enable the nectar, secreted by a ring-like nectary at the base of the style, to be reached by all except the shortest-tongued insects; but even in longer-tubed flowers the tubes are so narrow that the nectar rises in them and is accessible to long-tongued flies and short-tongued bees. The flowers therefore are visited by a large variety of insects. In long-tubed forms, like the thistles, pollination is usually effected by bees and butterflies; in short-tubed forms, like the milfoil, by flies. *Artemisia* (mugwort, wormwood) is peculiar in having flowers adapted to wind-pollination.

A few interesting arrangements may be specially noticed. In the sunflower (*Helianthus annuus*) the *ligulate* ray-florets are neuter, as are also the *tubular* ray florets of the cornflower. In the coltsfoot (*Tussilago Farfara*) the tubular disc-florets are male, the ray-florets female. The flowers appear in spring before the leaves. The male flowers have a style, acting as a pollen-brush, but no stigmas. Both kinds of flower have a pappus, but it remains small in the male flowers. Only the male flowers secrete nectar. The butterbur (*Petasites hybridus*) is closely allied to the coltsfoot. It is dioecious, the tubular florets in the capitula being all male or all female. The male flowers have ovary and style, but no ovule.

A study of the floral structure, of the inflorescence, and of the arrangements for the dispersal of fruits in the Compositae supports the view that they represent the highest development amongst the flowering plants. The capitulum is a highly specialised inflorescence, and shows considerable division of labour. The aggregation of *small* flowers not only serves to attract insects with the least expenditure of material, but also secures the pollination of a number of flowers at each insect-visit.

Frequently, only some of the flowers (ray-florets) develop large corollas; this seems to be done at the expense of one or both sets of essential organs, hence the frequent occurrence of pistillate or neuter florets in the ray. There is little chance of fertilisation failing to take place. The ripening fruit, like the young flower, is protected by the involucre. The pappus provides for the wide dissemination of fruits by air currents. Some genera show parthenogenesis, *i.e.* the ovum develops into an embryo without fertilisation (*Hieracium, Taraxacum, Antennaria*).

The Compositae are divided into two sub-families—

(1) The *Tubuliflorae*, in which some, at least, of the flowers are tubular; there is no latex but schizogenous oil-ducts may be present. There are two common arrangements: (*a*) the flowers are all tubular, as in the thistles, but the outer ones may be larger and neuter; (*b*) there are ray and disc florets—those of the disc tubular and usually hermaphrodite, those of the ray ligulate and usually pistillate (*gynomonoecious condition*), e.g. the daisy.

(2) The *Liguliflorae*, in which all the florets in a capitulum are ligulate and hermaphrodite (e.g. dandelion). They all have laticiferous vessels.

I. **Tubuliflorae.**—*Centratherum anthelminticum* is frequent on black cotton soil. The "seeds" are used as an anthelmintic and insecticide. A number of species of *Vernonia* occur, some quite common weeds, others large shrubs or small trees. *Elephantopus scaber* is a common weed of lawns and grass lands. Its large leaves lie flat on the ground and it has a tuberous root from which it regenerates when the shoot is removed. Another common weed is *Ageratum conyzoides*, goat-weed, introduced from tropical America. Numerous species are cultivated as ornamental plants. *Erigeron canadense*, Canadian fleabane, is believed to have spread from N. America. It is a widely distributed weed. *Conyza* has about 50 species in the tropics. *Blumea* is well represented in India by a number of annual herbs or small shrubs. *B. balsamifera*, S.E. Asia, yields a kind of camphor. *Xanthium strumarium* has monoecious heads, the male in the upper axils at the ends of the branches, the female below, two-flowered, enclosed in a prickly gamophyllous involucre which is 2-horned, from which only the styles project. The involucre is covered with hooked bristles, suited for animal dispersal. *Bidens pilosa*, Spanish needle, has achenes provided with a pappus of 2-4 barbed bristles by which it is distributed. *Cosmos sulphureus*, a Mexican plant, is cultivated and occurs wild as a garden escape. *Tithonea diversifolia*, the wild sunflower, is of Mexican origin. *Helianthus annuus* is the true sunflower whose fruits yield an oil. *H. tuberosus*, the Jerusalem artichoke, is cultivated for its stem tubers which contain inulin ("Jerusalem" is a corruption of the Italian *girasole*). *Dahlia* species are cultivated as ornamental plants and are propagated by root-tubers. They are native to Mexico. *Senecio* (incl. *Emilia*) is a large genus of herbs and shrubs of various habit, including climbers and xerophytes with fleshy stems or leaves, or with hairy or inrolled leaves. Several "ragworts" occur in India and the common groundsel (*S. vulgaris*) has established itself in hilly districts. *Cynara Scolymus* is the true or globe artichoke, the edible part being the tender inner involucral bracts. The blanched summer growth is also edible (chards). *C. Cardunculus* is the cardoon, of which the leaves are blanched and eaten like celery. *Cnicus Wallichii* is a tall thistle with pale purple flowers, growing on open downs. *Echinops echinatus* is a thistle-like herb in open situations in dry districts.

Carthamus tinctorius, kusum, safflower, is cultivated on account of the dye yielded by its flowers, and used by man from earliest times.

II. **Liguliflorae.**—*Lactuca* species grow wild on the plains and in the hills. *L. sativa*, lettuce, kahir, salád, is cultivated. *Launea pinnatifida* is a trailing plant common on sandy seashores and useful as a sand binder. *Cichorium Intybus* is the wild chicory, also cultivated for its root which is roasted and blended with coffee. *C. Endivia* is the endive, a salad plant native to the Mediterranean region. *Picris, Crepis* and *Sonchus* species occur in the hills, and also the dandelion, *Taraxacum officinale*, whose root is used in medicine.

Many Compositae are cultivated besides those mentioned above. These include species of *Zinnia, Coreopsis, Tagetes, Gaillardia, Chrysanthemum, Calendula* and *Callistephus*.

PART III—VASCULAR CRYPTOGAMS AND FLOWERING PLANTS

CHAPTER XIV

PTERIDOPHYTA

1. It is necessary to study several types if we wish to obtain a clear idea of the characters and course of the life history in Vascular Cryptogams, and if we wish, further, to trace the morphological and developmental resemblances, *i.e. homologies*, which exist between them and the Spermatophyta. The life histories of the fern, horse-tail (*Equisetum*), and *Selaginella* will have to suffice for our purpose.

A. LIFE HISTORY OF THE FERN

2. General Characters

The ferns are by far the most important group of the Pteridophyta or Vascular Cryptogams. Many are shade- and moisture-loving plants, and grow abundantly in woods, hedges, and on hill-sides. Some, however, are xerophilous, and in the tropics there are epiphytic forms.

The fern plant shows a well-marked differentiation into root, stem, and leaf. The stem has various forms—e.g. in the tree ferns of the tropics it is aerial, erect, and unbranched; but in most cases it is a *rhizome*, growing either horizontally or obliquely upwards through the soil. The roots are fibrous and *adventitious*, being developed from the surface of the rhizome or from the leaf-bases. The leaves are generally large and highly developed. The lamina is sometimes entire (e.g. the hart's-tongue fern) but is usually much divided.

To illustrate the structure and life history of the group, we shall consider more especially *Dryopteris Filix mas*, the male shield fern. Reference, however, will also be made to *Pteridium aquilinum*, the common bracken. Both of these ferns occur in India.

3. Rhizome, Leaf, and Root

The **rhizome** of *Dryopteris* (Fig. 284) is obliquely ascending to almost erect, its apex just reaching the surface of the ground. It is fairly stout and is covered by numerous persistent leaf-bases. There is usually no lateral branching, but adventitious buds may be developed on the bases of the leaves, and these may separate to form new plants. Lateral branching occurs in many ferns, but it is rarely truly axillary. As the rhizome grows forward, it gradually decays and dies off behind; in this way the adventitious buds or the lateral branches become separated, and form independent rhizomes.

The **leaf** is large and compound bi-pinnate. The petiole is continued upwards as the *rachis*, which bears the green, flattened pinnae which are further divided into pinnules. A rosette of leaves unfolds each year, but each leaf takes two years to develop. All the young leaves and the bases of the old leaves are covered with

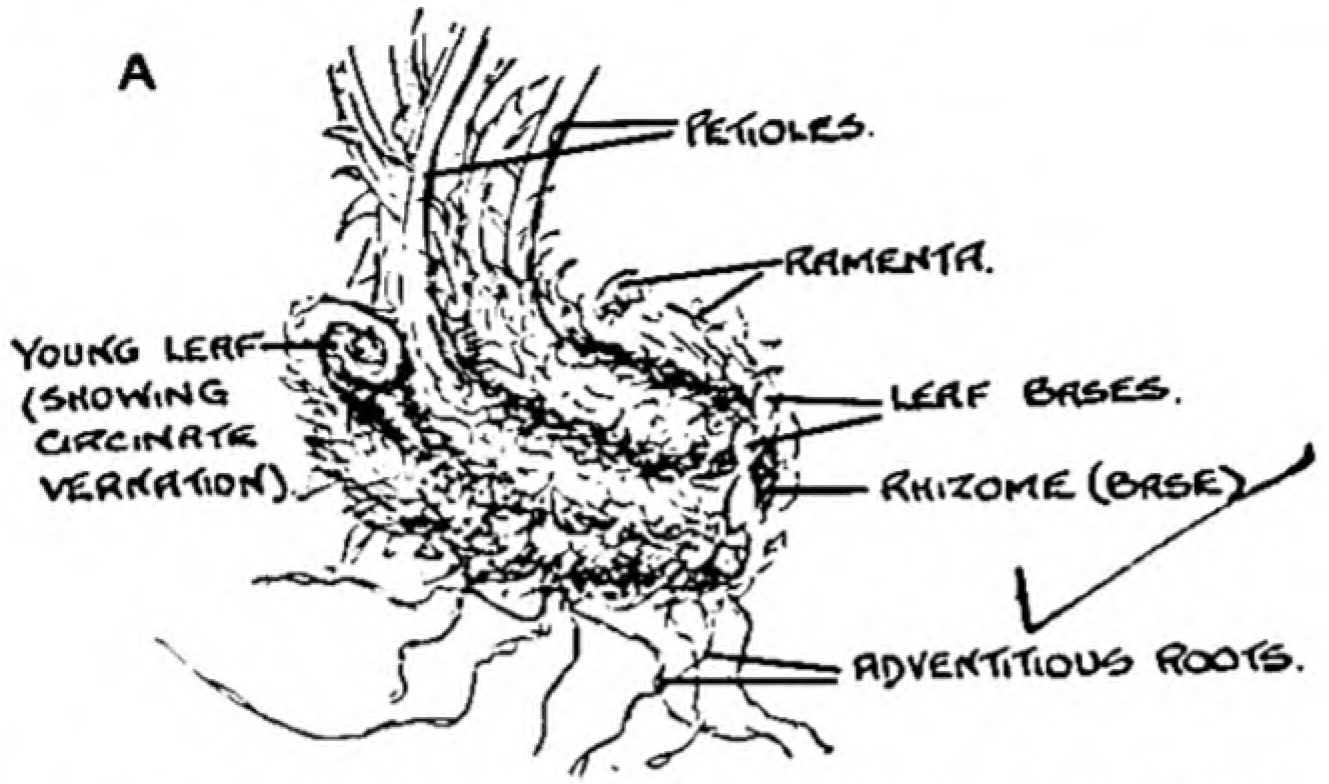

Fig. 284, A. External View, Rhizome of Male-Fern.

① numerous brown ramenta (p. 54), which are characteristic of ferns in general. The *ptyxis* of the leaf is circinate (p. 136); this also is ② characteristic; each leaf is rolled on itself like a crosier from the apex to the base. The venation is described as *furcate* or divergent. ⑤ One main vein enters each pinnule and gives off branches, which bifurcate and end near the margin without anastomosing.

The **fibrous adventitious roots** are developed chiefly from the bases of the leaves.

The dorsiventral rhizome in bracken is elongated and grows horizontally through the soil, branching at intervals. The branching is really lateral, but simulates dichotomy. As in *Dryopteris*, adventitious buds are developed at the bases of the petioles. Only one leaf is unfolded each year on each branch of the rhizome. It unfolds in the spring of the third year after beginning its development. The leaves are separated by long internodes. The rachis is branched. In some ferns adventitious buds are developed on the upper surface of the lamina They may separate, strike root, and form new plants.

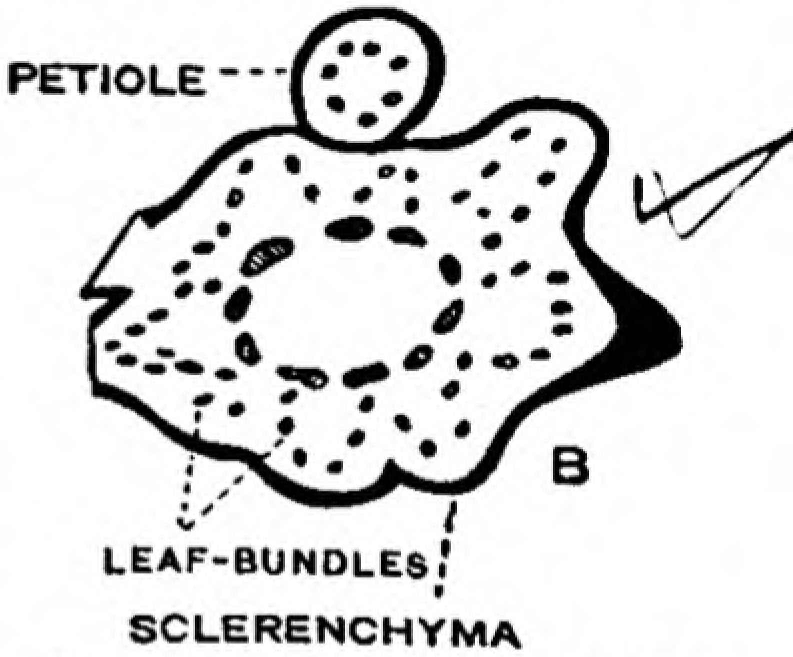

Fig. 284, B. T.S. Rhizome of Male-Fern (Diagrammatic).

4. Structure of the Rhizome

Fig. 284, B, represents a transverse section of the rhizome of *Dryopteris*. It shows a series of meristeles arranged in a ring. The ground-tissue is chiefly parenchymatous, but there is a hypodermal band of sclerenchyma. In the ground-tissue outside the ring there is a number of small traces passing out to the leaves.

From the cells of the ground tissue of male-fern, bordering the large intercellular spaces grow unicellular, glandular hairs, having a narrow stalk and a globular head secreting a resinous substance (Fig. 29, F). The resin is used therapeutically for the expulsion of tape-worm.

Fig. 285 shows a portion of the vascular system isolated. The meristeles fuse at intervals and form a cylindrical network surrounding the pith. The meshes of the network correspond to the insertion of the close-set leaves, and are therefore called the *foliar gaps*. The traces passing out to the leaves are given off as branches from the edges of the foliar gaps. There is no secondary growth.

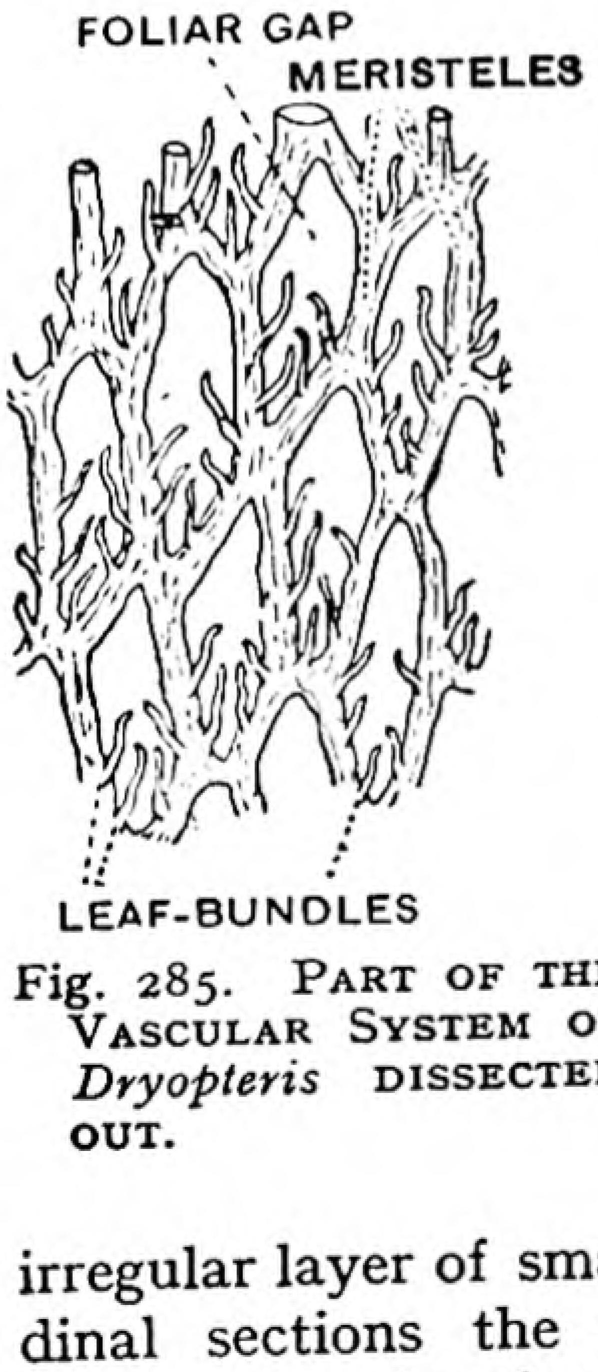

Fig. 285. PART OF THE VASCULAR SYSTEM OF *Dryopteris* DISSECTED OUT.

5. Structure of the Meristele

The outline of the meristele in transverse section (Fig. 286) is more or less round to elliptical. In the middle is the **xylem** consisting chiefly of long slender scalariform tracheides (Fig. 24) and small-celled *xylem parenchyma* containing starch. The meristele, according to size, may have one, two, or three **protoxylem** groups. These consist of small spiral tracheides. Frequently a group is found at each end of the xylem.

The xylem is *surrounded* by the **phloem.** This consists of a layer of sieve-tubes with associated parenchymatous cells (phloem parenchyma), and, outside this, a narrow irregular layer of small fibrous cells, the **protophloem.** In longitudinal sections the sieve-tubes are seen to consist of narrow elongated pointed cells with protein contents. The sieve-tubes contain no starch; numerous *sieve-plates* are present on their lateral walls only; there are *no companion cells.* These features are characteristic of ferns.

Outside the protophloem are the **pericycle** and **endodermis.** Typically each of these consists of a single layer (Fig. 289); but in *Dryopteris* and some other ferns, the endodermis is double round the greater part of the meristele (Fig. 286). The cells of the pericycle and inner layer of the endodermis contain starch. The outer layer of the endodermis consists of cells thickened as in a typical endodermis.

6. The Stelar System in Ferns

The simplest type of vascular structure met with in the stem of ferns is the **Protostele**, consisting of a solid mass of xylem (or xylem mixed with parenchyma) *completely* surrounded by phloem, pericycle and endodermis in regular order, as shown in Fig. 287, A. The vascular supply of the leaf (*leaf-trace*) comes off as a small strand (also consisting of xylem surrounded by phloem, pericycle and endodermis), which may be either rod-like (Fig. 287, A), or gutter-shaped with the concavity turned towards the stem.

Other ferns possess a **Solenostele**, which is a tube of xylem lined *both internally and externally* with phloem, pericycle and endodermis, these tissues occurring in the reverse order on the inside (Fig. 287, B), so that the internal endodermis immediately surrounds a pith which occupies the centre of the stele. The leaf-trace in these solenostelic ferns usually arises as a single gutter-shaped strand (Fig. 287, B, *b*), which higher up in the leaf may divide into several strands. But an important fact is that there is almost always a gap in the xylem tube just in front of an off-coming leaf-trace. This gap is called a *leaf-gap* or *foliar gap*; it closes up some distance in front of the leaf-trace. At the margin of the gap the internal endodermis, pericycle and phloem meet the corresponding external tissues, and place the central pith into communication with the cortex of the stem. Hence if we dissect out only the xylem portion of such a stem we obtain a hollow cylinder which is perforated by an elongated gap wherever a leaf arises. A transverse section of such a cylinder, therefore, is either **C**-shaped or **O**-shaped according as it does or does not pass through a leaf-gap.

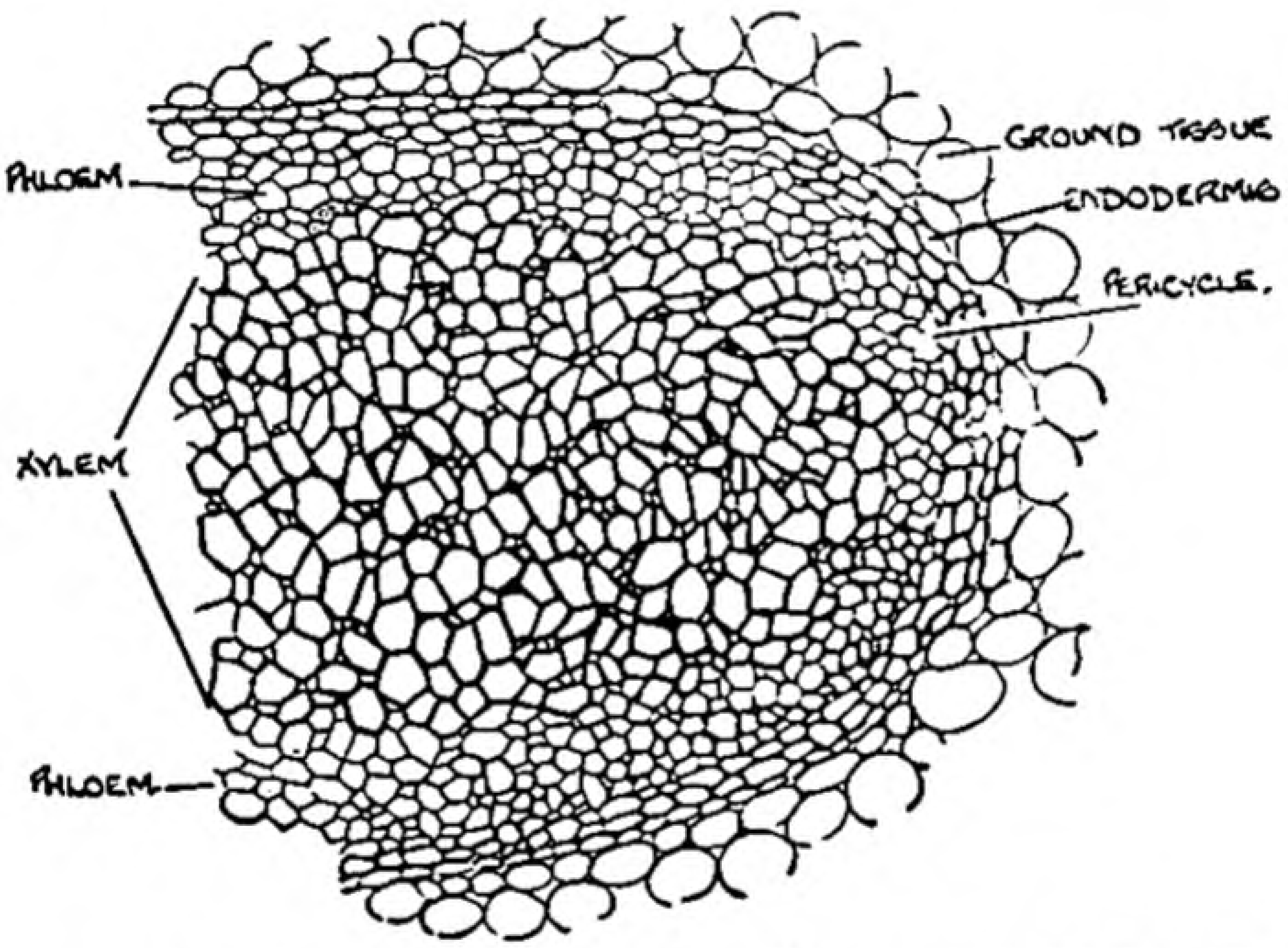

Fig. 286. *Dryopteris*. PART OF MERISTELE IN DETAIL.

In solenostelic ferns the leaves usually do not arise at short intervals, so that the leaf-gaps do not overlap. No single transverse section will pass through more than one gap; on the other hand many of the sections will be gap-less (O-shaped). If, however, we imagine the leaves to be crowded together on the stem, each leaf producing a gap in the vascular cylinder, we obtain a

Dictyostele, so called because of the net-like character of the cylinder (Fig. 287, *c*, and Figs. 284 and 285). The leaf-trace is usually compound, that is, it consists of several small strands. These are as a rule clearly arranged in an arc, and are together equivalent to the undivided C-shaped trace of the solenostelic ferns. In a dictyostele the leaf-gaps are so crowded that it is impossible to avoid cutting several (at least two) of them in the same transverse section; hence such a section shows the cylinder broken up into a ring of smaller strands (*meristeles*), each resembling a miniature protostele.

Of the three main types of vascular system above described, the protostele is generally met with in *Hymenophyllum*, *Trichomanes*, *Gleichenia* spp., *Lygodium*; the dictyostele in many Polypodiaceae, such as *Dryopteris*, while a large number of ferns are solenostelic.

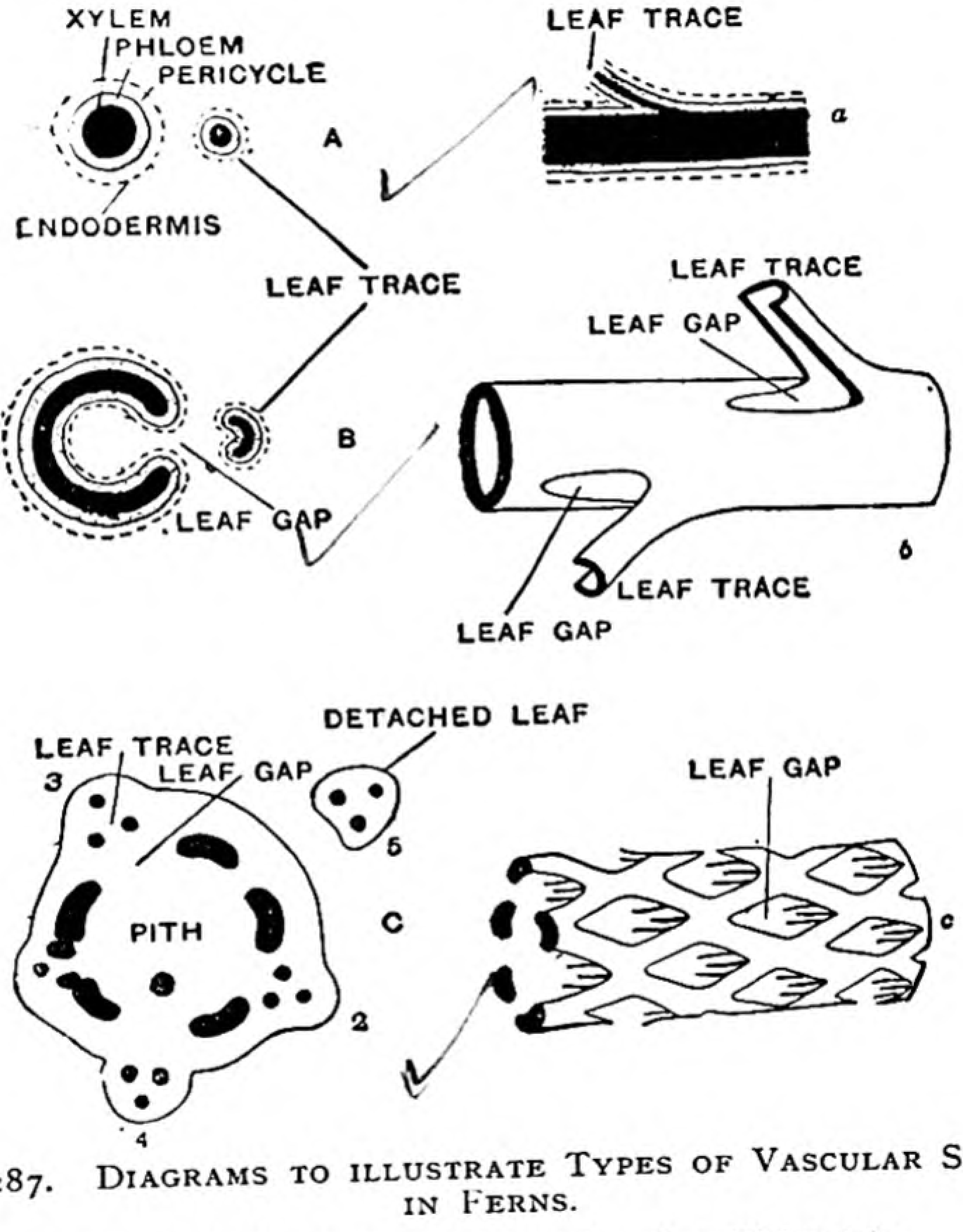
XYLEM
PHLOEM
PERICYCLE
ENDODERMIS
A
LEAF TRACE
a
LEAF TRACE
LEAF TRACE
LEAF GAP
B
LEAF GAP
b
LEAF TRACE
LEAF GAP
DETACHED LEAF
LEAF TRACE
LEAF GAP
3
5
PITH
C
2
4
LEAF GAP
c

Fig. 287. Diagrams to illustrate Types of Vascular System in Ferns.

A, *a*, Protostele; B, *b*, Solenostele; C, *c*, Dictyostele.

There are also many ferns (e.g. *Pteridium aquilinum* and tree ferns) which do not quite agree with any of these three types.

Hitherto we have considered the stelar system of only the fully developed stems. But if we trace the development of a dictyostelic fern stem from its earliest stage to the adult condition, we generally find that the young sporophyte has a protostele. This protostele, as we trace it forwards into the later-formed parts of the stem, becomes hollowed into a solenostele, and finally, in the mature stem, there is a dictyostele. Thus in a dictyostelic fern a series of transverse sections from the base of the stem upwards will show, in turn, a transitory protostele, a transitory solenostele, and a permanent dictyostele. This is regarded as supporting the **Recapitulation Theory,** according to which an organism during its individual life-time more or less closely recapitulates the history of its race.

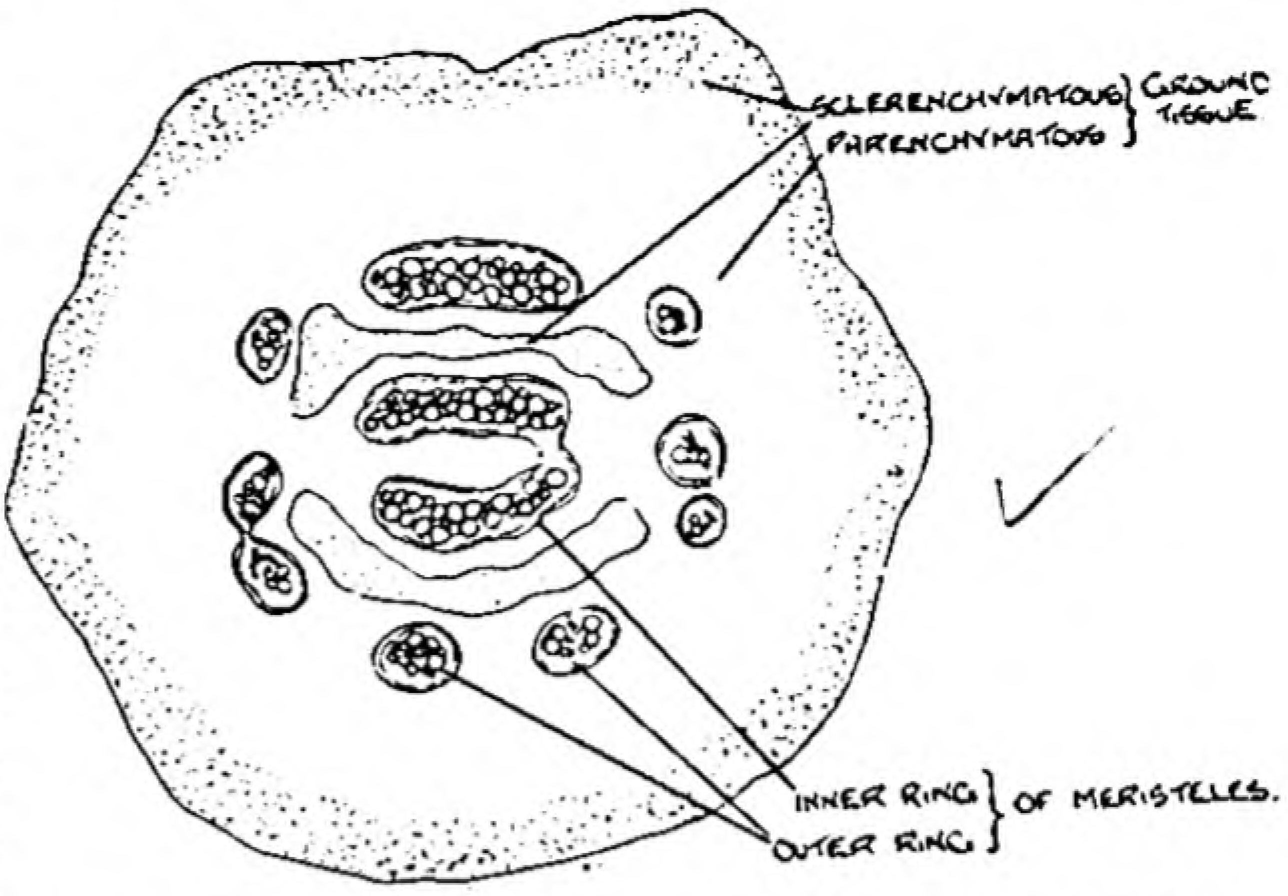
SCLERENCHYMATOUS } GROUND TISSUE
PARENCHYMATOUS
INNER RING } OF MERISTELES.
OUTER RING

Fig. 288. TRANSVERSE SECTION, RHIZOME OF *Pteridium.*

7. The Bracken Fern

In the bracken fern (Figs. 288 and 289) there are two series of meristeles, between which lie two stout bands of sclerenchyma. The outer meristeles are more numerous, but smaller. The hypodermal sclerenchyma does not form a continuous band; it is interrupted on each side of the rhizome, and the

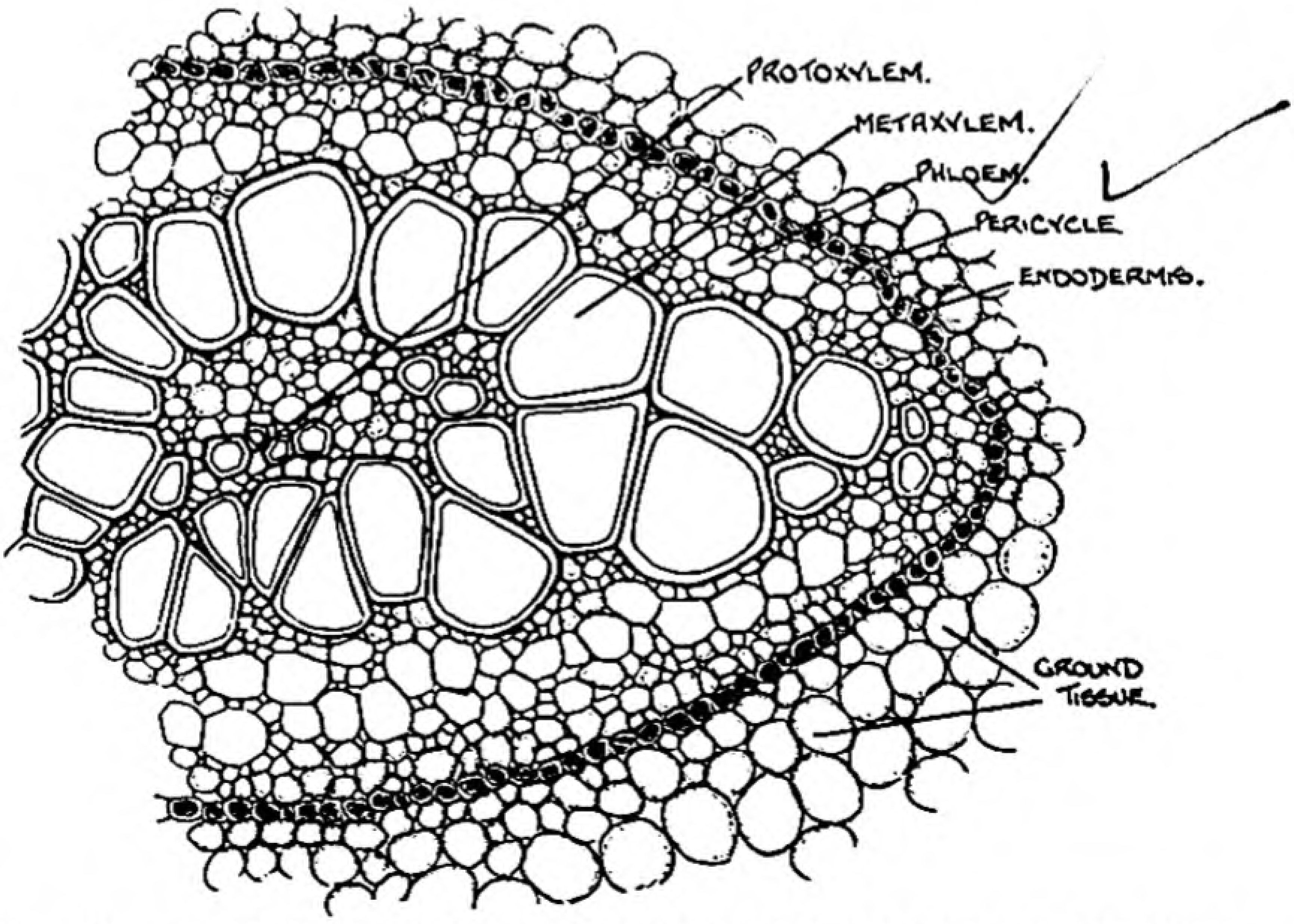
PROTOXYLEM.
METAXYLEM.
PHLOEM.
PERICYCLE
ENDODERMIS.
GROUND TISSUE.

Fig. 289. TRANSVERSE SECTION, PORTION OF MERISTELE OF *Pteridium.*

parenchymatous ground-tissue reaches the epidermis. It can be seen externally as a lighter coloured line on each flank of the rhizome, and it may be concerned with the proper aeration of the tissues. A regular cylindrical network of meristeles is usually not found in ferns with dorsiventral rhizomes (bracken, etc.). The leaves are few in number, and the foliar gaps are very much elongated. Thus the meristeles form long, irregular strands, which fuse only at considerable intervals.

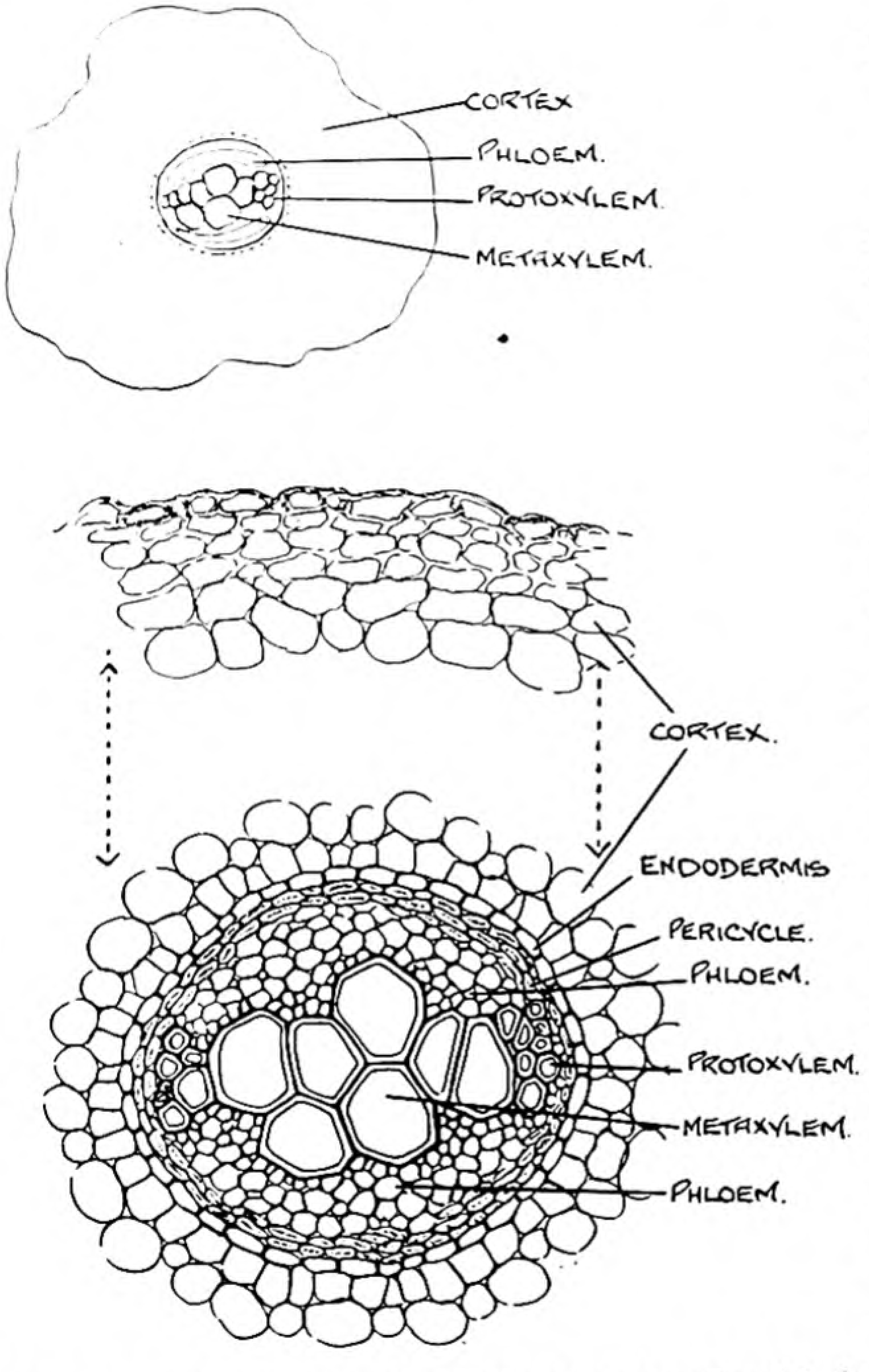

Fig. 290. TRANSVERSE SECTION, ROOT OF *Dryopteris.*

8. Structure and Development of the Root

The root contains a number of xylem and phloem strands situated on alternate radii. In *Dryopteris* and most other ferns the stele is *diarch* (Fig. 290). The pericycle and endodermis are single layers of thin-walled cells. In the older parts of the root the cortical tissue immediately outside the endodermis is usually strongly lignified, and forms a stout strengthening sheath. The outer cortical tissue is parenchymatous. The outermost layer is the piliferous layer. There is no secondary growth.

Lateral branch-roots, while they are *endogenous* in origin, are not developed, as in Spermatophyta, from the pericycle, but from the endodermis. They arise opposite the protoxylem. In the same way the adventitious roots developed from the rhizome or petiole take their origin in the endodermis investing a meristele.

9. Apex of Rhizome and Root (Fig. 291)

At the apex of the rhizome there is, as in Spermatophyta, a mass of meristematic tissue. An important difference, however, must be noticed. In ferns there is at the apex one large distinct cell from which all the tissues are produced. This is the **apical cell.**

In the rhizomes of most ferns (e.g. *Dryopteris*) this cell is bounded by four walls—three flat walls meeting in a point below, and a curved wall closing in the cell on top. The cell, therefore, is tetrahedral in form, its apex being directed inwards. Segments are cut off, *in succession*, parallel to the flat walls. After the formation of each segment, the apical cell increases to its original size. The segments are indicated in the figure. There are no segments cut off parallel to the curved wall in the rhizome.

In ferns with distinctly dorsiventral rhizomes (e.g. bracken) there is a two-sided instead of a three-sided apical cell, and there are, therefore, only two instead of three series of segments.

The segments cut off undergo division, and thus the tissues of the rhizome are produced. The first division is into inner and outer segments (Fig. 291, A). The tissue formed by division of the outer segments gives rise to the cortical ground tissue and the outermost layer is specialised to form the protective external covering, the epidermis of the rhizome. All the vascular strands make their appearance in the tissue which is formed from the inner segments. The layer of ground-tissue immediately surrounding each vascular strand forms an endodermis.

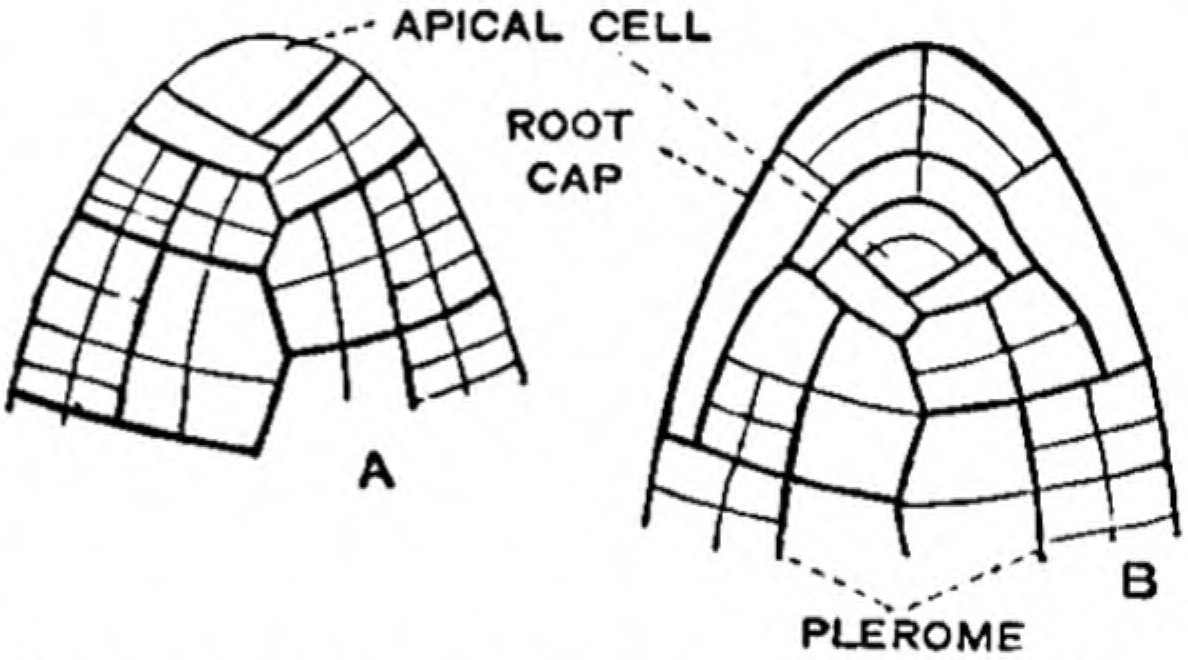

Fig. 291. APEX OF A, RHIZOME AND B, ROOT OF FERN.

(Diagrammatic longitudinal sections.)

In the **root,** also, there is a single apical cell. It lies just behind the root-cap. In all cases it is three-sided. The segments cut off parallel to the flat walls divide in the same way as in the rhizome; here also the inner segments give rise to the tissue from which the vascular cylinder is developed. Segments are also cut off parallel to the curved wall, and give rise to the root-cap. The tissue of the root-cap does not persist behind the apex.

10. Structure and Development of the Leaf

The leaf is developed exogenously from a single superficial cell of the growing point. This cell persists at the apex of the leaf as a two-sided apical cell until an adult condition is reached. A number of vascular strands enter the petiole from the rhizome (Figs. 284, B and 285). These branch out into the pinnae, where they maintain their concentric structure; but in the pinnules they break up into bundles which are more or less collateral. As is usual in shade-loving plants the palisade and spongy layers of mesophyll are not very sharply differentiated, and the ordinary epidermal cells have chloroplasts. Stomata are confined to the lower surface of the leaf.

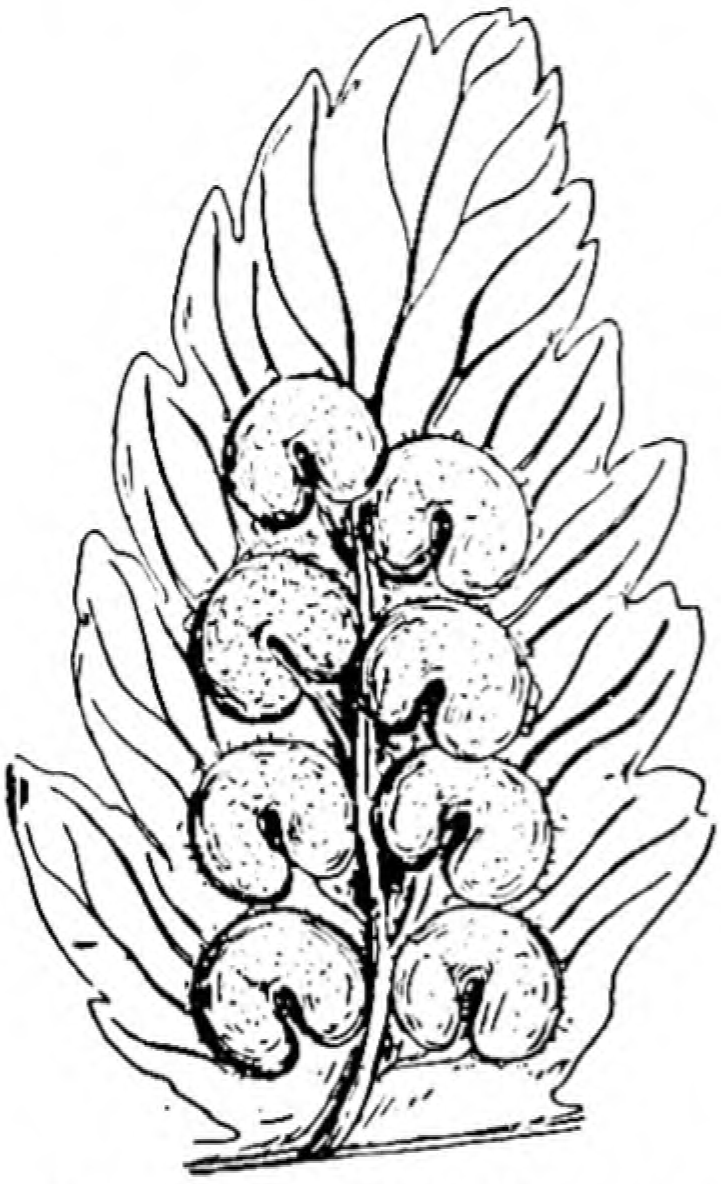

Fig. 292. PINNULE OF *Dryopteris* BEARING SORI.

11. Sporangia and Spores

Early in the summer a number of structures called **sori** appear on the under surface of the pinnules of the leaves of *Dryopteris*. These are at first of a light green colour, but when older they become dark brown (Fig. 292). They are developed immediately over the veins.

If a young sorus is removed and examined with a lens, it will be found to consist of a collection of very small stalked bodies called **sporangia** which are covered over and protected by a horse-shoe-shaped scale called the **indusium.** The sporangia and indusium are together developed on a little cushion of tissue, the **placenta,** formed immediately over a vein. The relative positions of these various parts is shown in Fig. 293, A and B, which represents a transverse section of a pinnule passing through a sorus. In some ferns (e.g. *Polypodium*) the groups of sporangia are not covered by an indusium. A sorus, therefore, may be described

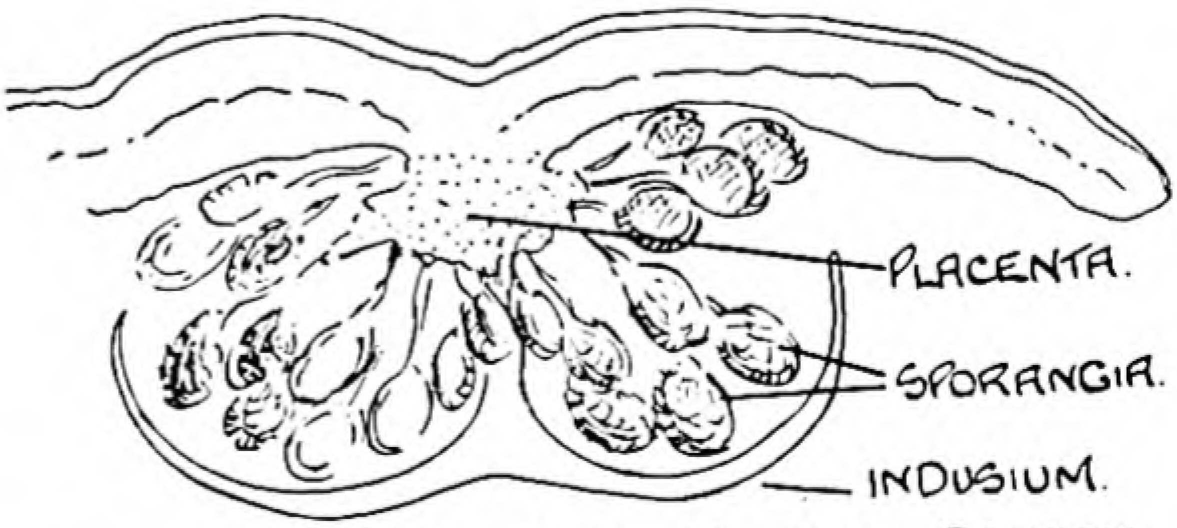

Fig. 293, A. *Dryopteris*, VERTICAL SECTION, SORUS.

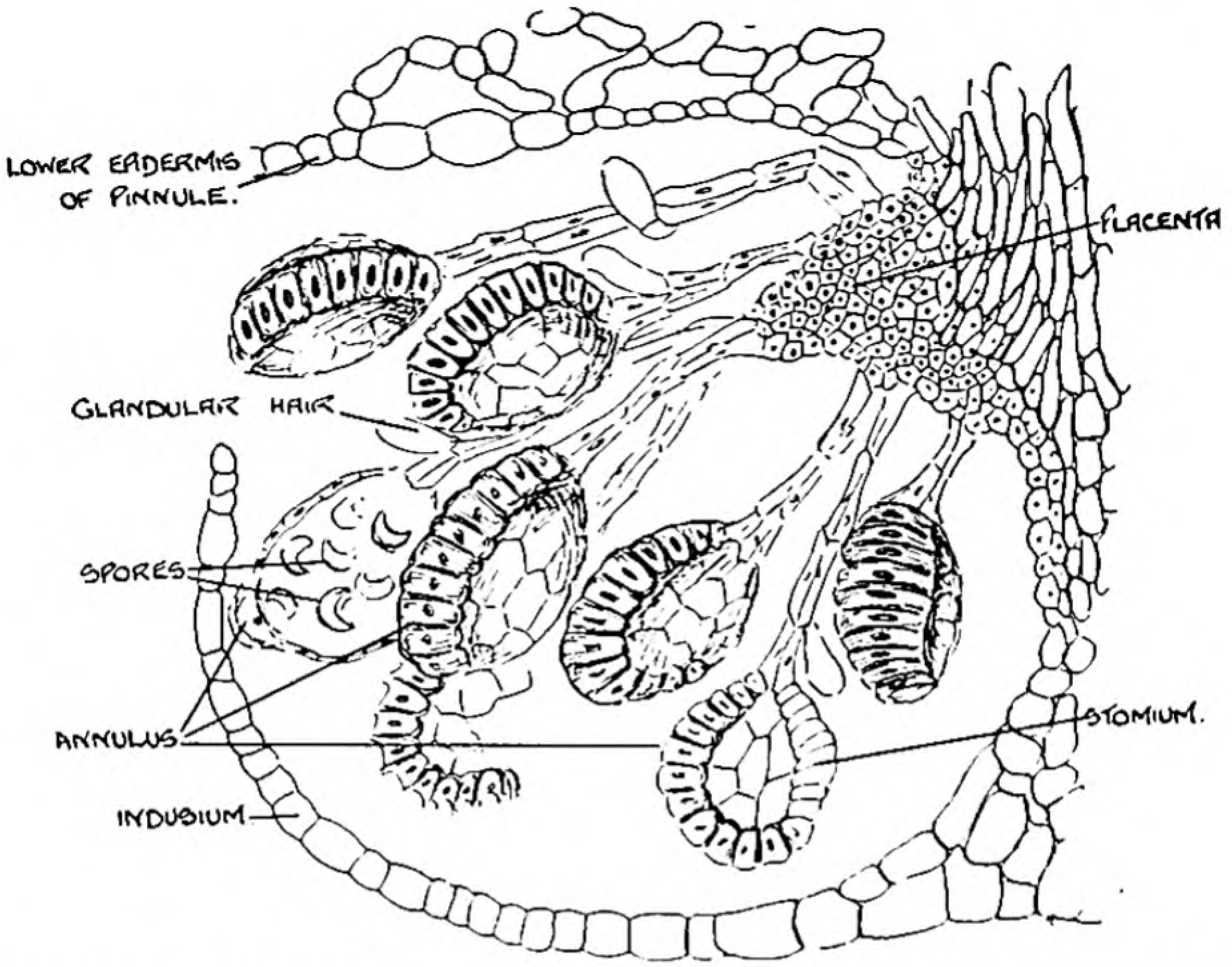
LOWER EPIDERMIS OF PINNULE.
PLACENTA
GLANDULAR HAIR
SPORES
ANNULUS
STOMIUM.
INDUSIUM

Fig. 293, B. VERTICAL SECTION, PINNULE OF *Dryopteris* THROUGH SORUS.

as a collection of sporangia developed on a placenta, either with or without an indusium.

The mature sporangium (Fig. 294) is a small structure consisting of a capsule borne on a slender multicellular stalk. The stalk in *Dryopteris* often bears a glandular hair (Fig. 293), the function of which is doubtful. The capsule is biconvex, and its wall consists of a single layer of cells. The cells are small and thin-walled except round the edge of the capsule, where they are larger, and thickened on their lateral and inner walls. This specialised row is called the **annulus.** It extends from the stalk about three-quarters of the way round the edge of the sporangium, and terminates near the *stomium* cells, characteristically shaped which together with the annulus are concerned in the dehiscence of the sporangium.

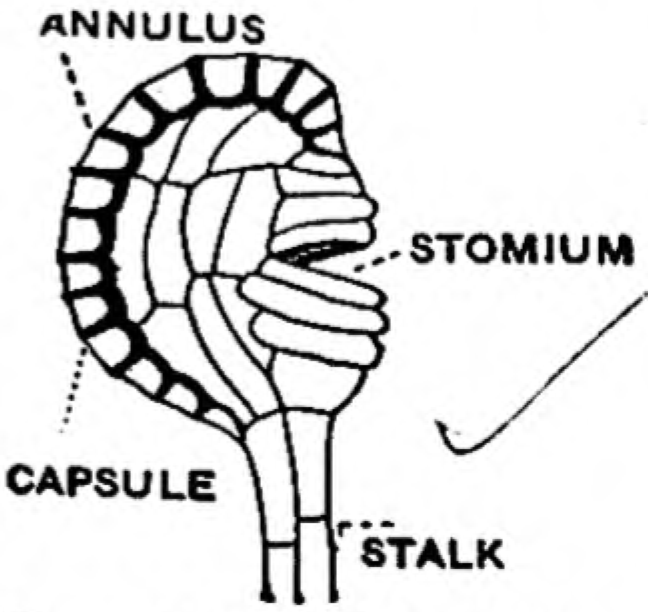
ANNULUS
STOMIUM
CAPSULE
STALK

Fig. 294. SPORANGIUM OF FERN.

Inside the sporangium lies a loose powder which on examination is found to consist of extremely small **spores.** In many ferns sixty-four of these are produced inside each sporangium; but there are usually only forty-eight in *Dryopteris*. The spore, which is of a brown colour and irregular or somewhat triangular in shape, is a single cell consisting of cytoplasm and nucleus invested by a double cell-wall, the outer of which is thickened.

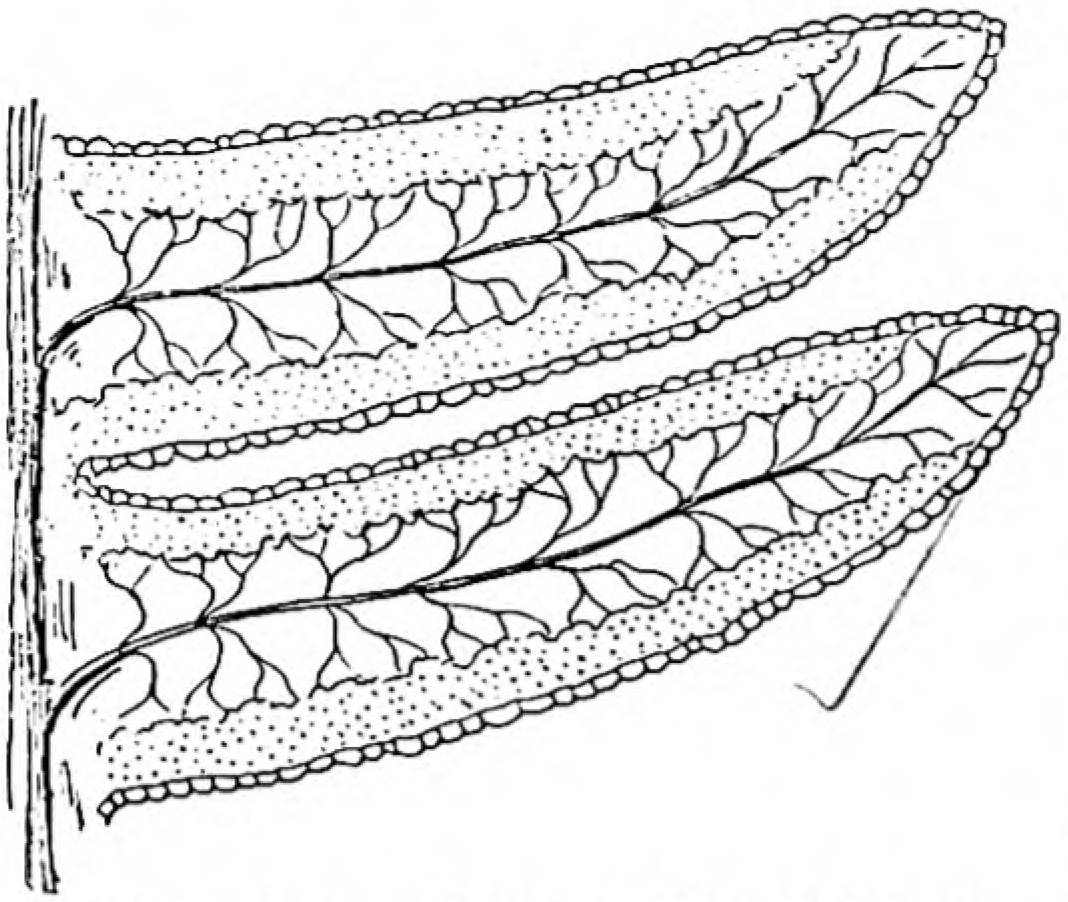

Fig. 295, A. Fertile Pinnules of *Pteridium*.

Pteridium (Fig. 295).—The sporangia and spores have the same structure and appearance as in *Dryopteris*, except that no glandular hair is developed on the stalk of the sporangium. The sporangia, however, are differently arranged. Instead of being grouped together in small sori, they are developed in a continuous series on a placenta running along the under margin of the pinnule. In other words, there is a continuous linear sorus. On the inner side of the placenta in the common bracken there is a delicate indusium. The margin of the pinnule also, by bending over, serves to protect the sporangia, and is termed a *false indusium.*

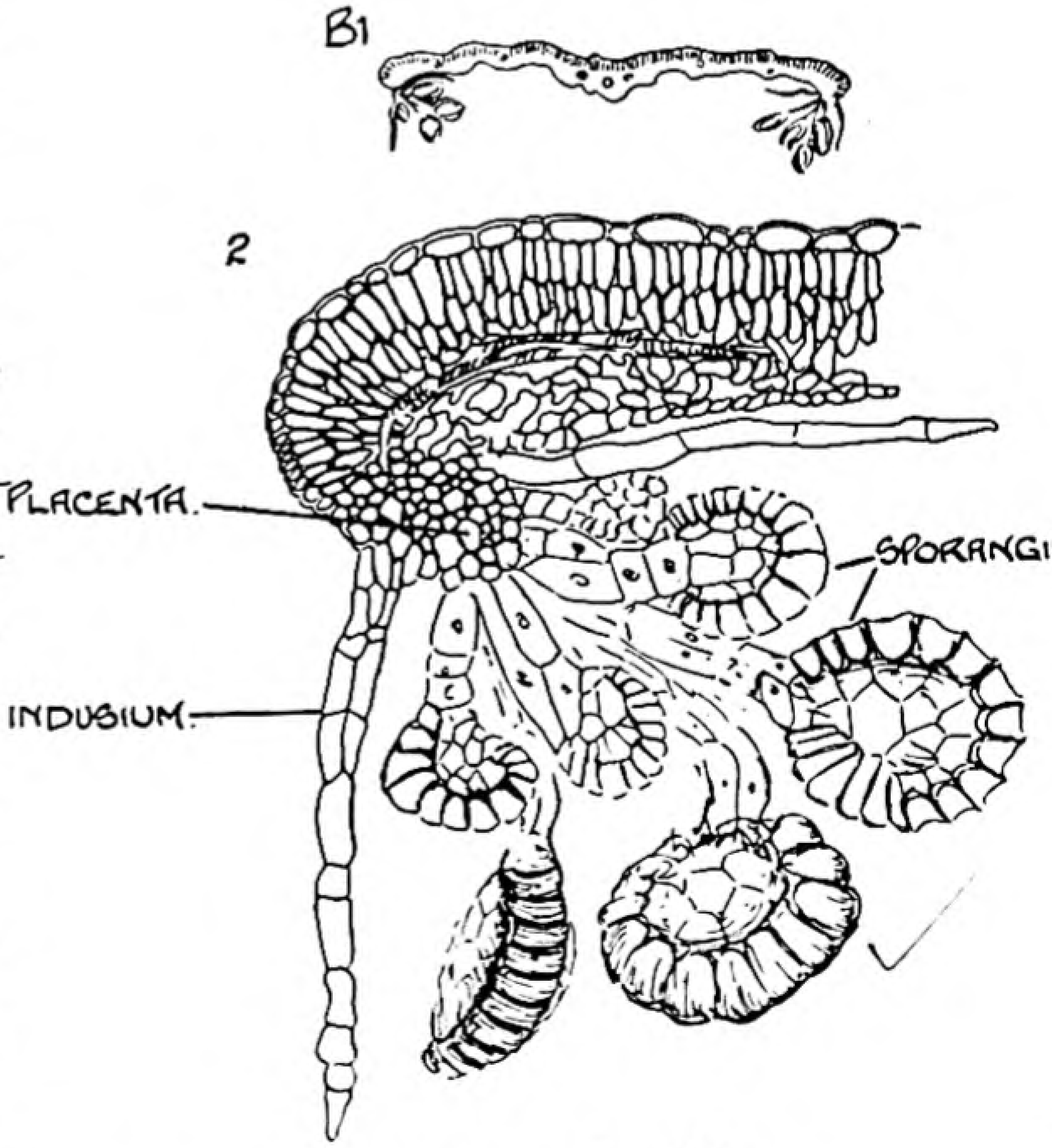

Fig. 295, B. *Pteridium.*
Vertical Section; 1, Pinnule, diagrammatic
2, Sorus, in detail.

12. Development of the Sporangium (Fig. 296)

The sporangium is developed from a single epidermal cell of the placenta. The cell in question grows out and forms a protuberance,

16. The Prothallus

The prothallus is a very small flat plate of tissue, measuring only about one-third of an inch across. It consists of parenchymatous cells, containing numerous chloroplasts. Towards the margin these cells form a single layer, but in the central region there are several layers forming the *cushion*. Long, brown, unicellular **rhizoids** are developed from the cells of the under surface and serve to anchor the prothallus to the substratum, but the entire surface absorbs moisture. The prothallus is an independent plant; it can synthesise its own carbohydrates and absorb mineral salts from the substratum. Owing to its thinness gases can penetrate to all parts with relative ease.

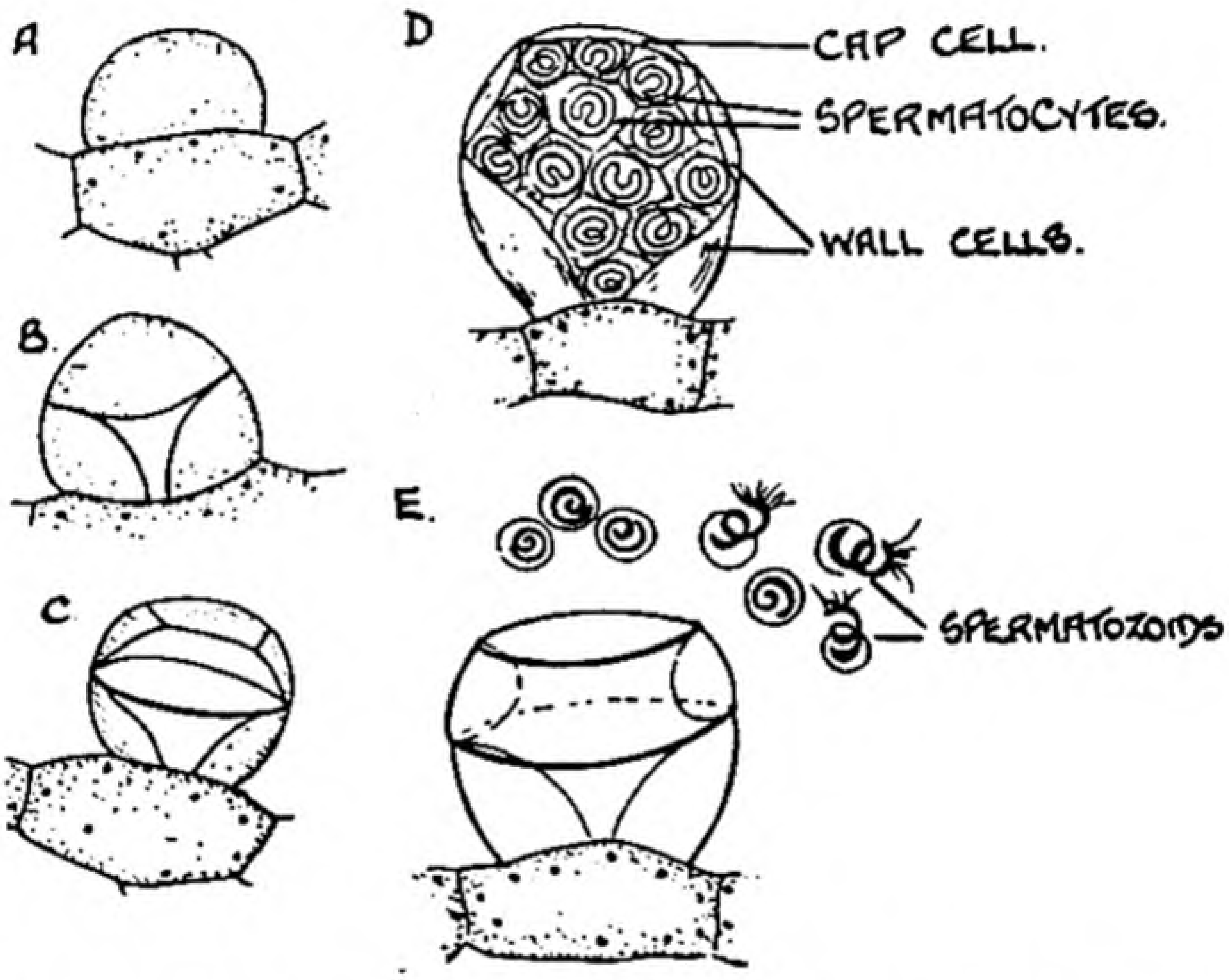

Fig. 298. Development of Antheridium of Fern.

17. The Sexual Reproductive Organs

These are produced on the *under* surface of the prothallus—the **antheridia,** or *male sexual organs,* on the posterior region, the **archegonia,** or *female sexual organs,* on the cushion in the anterior region near the notch of the heart-shaped prothallus (Fig. 297, c). The antheridia are developed first, whilst the prothallus is still young.

The *antheridium* (Fig. 298) is a spherical capsule, the wall of which consists of a single layer of cells containing chloroplasts. Inside are a number of small cells called **spermatocytes,** or *spermatozoid mother-cells,* each of which gives rise to a male gamete, the **spermatozoid.**

The *archegonium* (Fig. 299, E) is a flask-shaped organ, consisting of two parts: (*a*) a swollen basal portion, the *venter*, completely sunk in the tissue of the prothallus; (*b*) a more slender portion called the *neck*, projecting freely from the surface. The venter contains a single large **ovum**, or oosphere, which is the female gamete and has no cell-wall. The neck consists of four longitudinal rows of cells surrounding a central canal, which is at first closed at the apex, and which leads down into the venter. The neck is not straight, but bends towards the position of the antheridia. At the junction of the venter and the neck-canal there is another smaller nucleated protoplast, the **ventral canal-cell,** and the canal of the neck itself is filled with a protoplasmic mass containing several nuclei, which is called the **neck-canal-cell.**

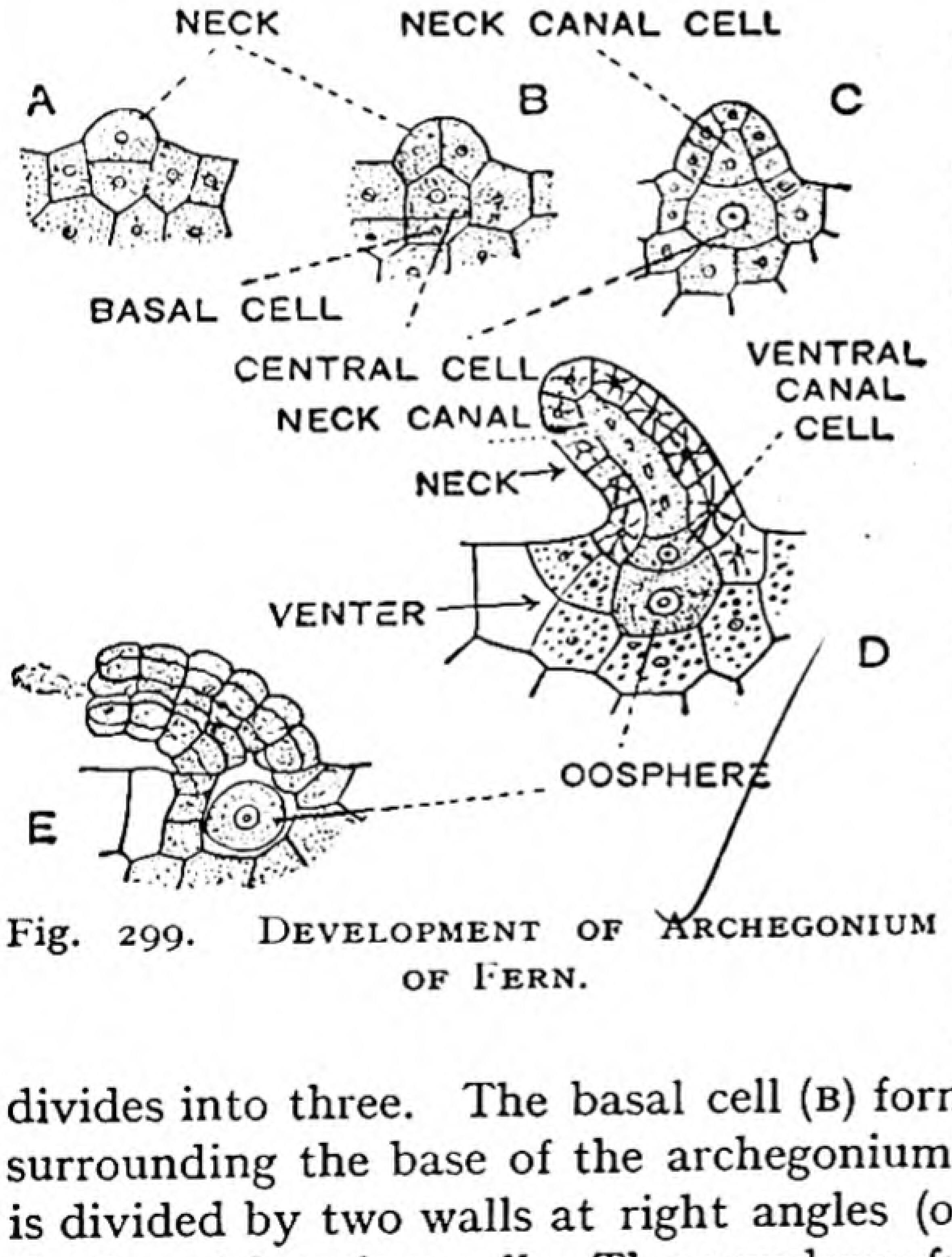

Fig. 299. DEVELOPMENT OF ARCHEGONIUM OF FERN.

18. Development

The *antheridium* (Fig. 298) is developed from a single cell of the prothallus. The cell grows out to form a papilla-like outgrowth which is cut off by a cell-wall. It increases in size, and two ring-shaped cells and a cap-cell, forming the wall, are marked off from a central cell in which the spermatocytes are formed.

The *archegonium* also is developed from a single cell (Fig. 299). This cell divides into three. The basal cell (B) forms a portion of the tissue surrounding the base of the archegonium. The outermost cell (B) is divided by two walls at right angles (only one can be shown in the figure) into four cells. These undergo further transverse divisions to form the four longitudinal rows of the neck (C-E). The protoplasm of the central cell (B) pushes its way between the neck-cells, and a small portion is cut off as the neck-canal-cell (C). The remainder of the protoplasm of the *central cell* undergoes division to form the oosphere and the ventral canal-cell (D). The cavity of the venter of the archegonium is partly lined by prothallus cells.

19. Fertilisation

When mature, the antheridium bursts open at the apex owing to absorption of water by the two ring-shaped cells forming the wall and the consequent pressure exerted by them on the contents of the antheridium (Fig. 298). The spermatozoid mother-cells are thus set free and the spermatozoids escape from them.

Each spermatozoid is a spirally coiled nuclear body bearing towards its slender anterior end a number of fine protoplasmic *vibratile* threads called **cilia**, whilst at the posterior end is a little vesicle, containing starch grains, and other unused remains of the spermatocyte.

The spermatozoids move about in the water by means of their cilia. Sooner or later they come into the neighbourhood of archegonia. When an archegonium is ripe the two canal-cells are disorganised and give rise to a mucilaginous substance which exudes from the now slightly funnel-shaped neck of the archegonium (Fig. 299, E). This substance contains malic acid. It diffuses into the water and attracts the spermatozoids (chemotaxis—see p. 228). They cluster round the neck of the archegonium, and, finally, one enters the canal, and passes down to the venter. It penetrates the oosphere and its nucleus fuses with that of the oosphere. The fertilised oosphere secretes a cell-wall and is then called the *oospore*.

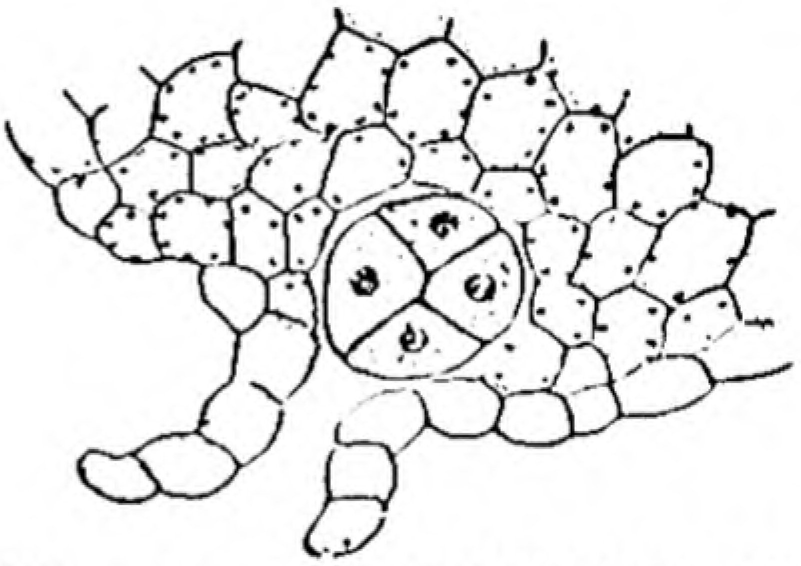

Fig. 300. SEGMENTATION OF OOSPORE OF FERN IN VENTER OF ARCHEGONIUM.

Although the prothallus bears as a rule both kinds of sexual organs, and is therefore hermaphrodite, cross-fertilisation generally takes place, the spermatozoids developed on one prothallus passing to the archegonia of another slightly older one. This is necessary because antheridia and archegonia are not developed simultaneously on a prothallus (cf. dichogamy, p. 260). Some prothalli, as a result of malnutrition, develop only antheridia.

20. Development of the Young Fern-Plant (Figs. 300 and 301)

The oospore, still within the venter, begins to divide or segment, and this process of segmentation leads finally to the development of an embryo. The first division-wall is nearly parallel to the long axis of the archegonium. It is called the **basal wall**, and divides the oospore into anterior or **epibasal** and posterior or **hypobasal** halves. A second wall, the transverse or quadrant wall, at right angles to the basal wall, divides the oospore into upper (superior) and lower (inferior) halves. The oospore now consists of four cells (quadrants). Then a median or octant wall at right angles to the first two divisions divides the oospore into right and left halves. The oospore now consists of eight cells or **octants** (Fig. 300).

Of the two superior anterior octants one becomes the apical initial cell of the **primary stem,** the other takes no special part in the development. The two inferior anterior octants give rise to the first leaf or **cotyledon.** Of the two inferior hypobasal octants, one becomes the apical cell of the **primary root**: it is diagonally opposite the cell which produces the primary stem. The two superior hypobasal octants give rise to an embryonic organ called the **foot.** This is a massive structure which absorbs nourishment from the prothallus for the developing embryo, till the latter can become independent.

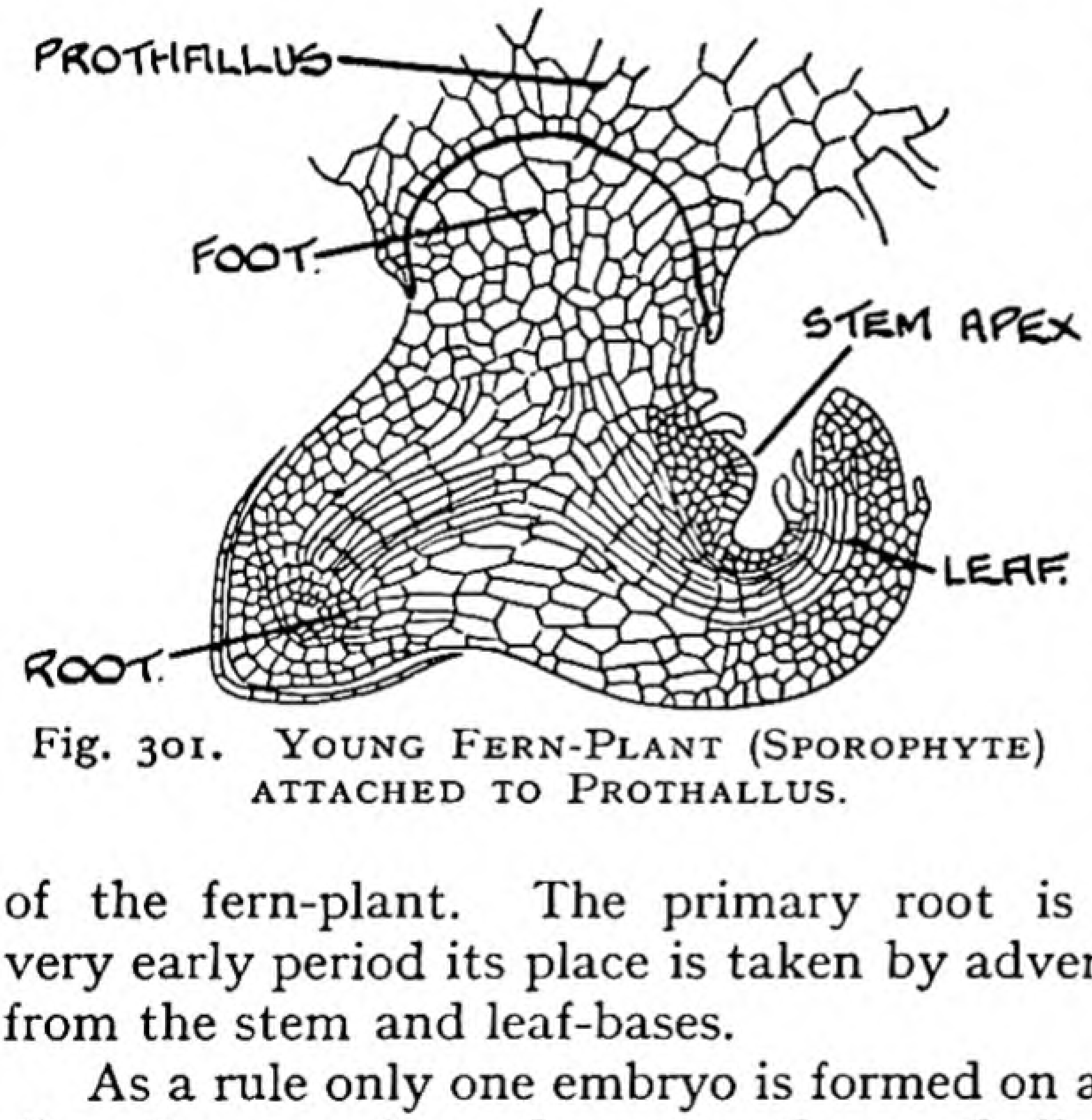

Fig. 301. YOUNG FERN-PLANT (SPOROPHYTE) ATTACHED TO PROTHALLUS.

Further cell-division, of course, takes place in the octants marking out the stele of root and stem. The primary stem and cotyledon appear from the under surface of the prothallus, then bend upwards, make their way through the notch of the prothallus and come above ground, where they become green. New leaves are developed, and gradually the stem becomes the rhizome of the fern-plant. The primary root is not persistent. At a very early period its place is taken by adventitious roots developed from the stem and leaf-bases.

As a rule only one embryo is formed on a prothallus, which then dies. In some ferns, however, the prothallus has a longer life, and may reproduce itself vegetatively by means of branches, or little outgrowths of meristematic tissue called gemmae.

21. Sporophyte and Gametophyte. Alternation of Generations

It will be noticed that in the life history of the fern there are really two plants to be considered. These are spoken of as the two *stages* or *generations* of the life-cycle. There is the fern-plant, so called because it is by far the more conspicuous of the two. It is named the **sporophyte** or asexual generation, because it is the generation which bears the asexual spores. Then there is the prothallus, specialisation and aggregation of sporophylls should be carefully noticed. The reproductive region of the shoot is quite distinct from the vegetative portion (see p. 7).

Under the peltate end of each sporophyll and surrounding the stalk are the **sporangia** containing spores. Each sporangium is developed from *a group of cells*, although all the essential parts are derived from a single superficial cell. After the wall of the sporangium and the tapetal layers have been formed a single large **archesporial cell** remains, which divides to form spore-mother-cells. These undergo meiotic division to form tetrads of spores.

The strobili or cones of *Equisetum* are borne either at the apices of ordinary vegetative shoots, or, in some species, on special fertile or reproductive shoots which resemble the others except that they are unbranched and contain little or no chlorophyll.

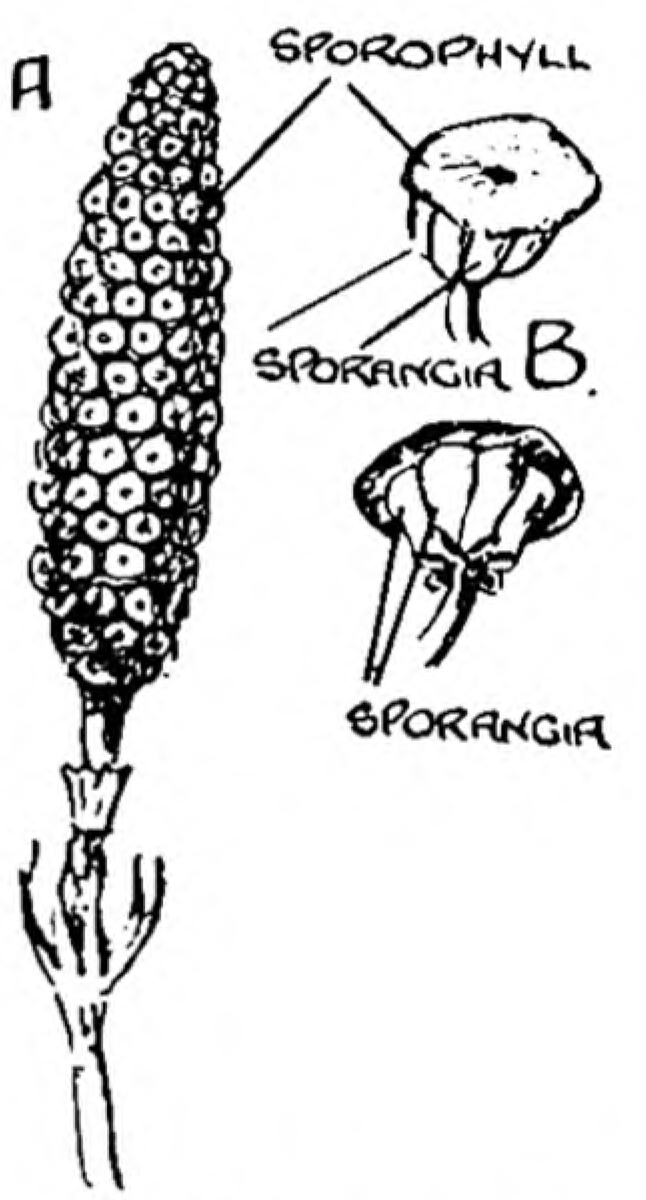

Fig. 303. *Equisetum.* A, Cone; B, Sporophyll, two views.

24. General Life History

On maturing, the peltate sporophylls become concave, thus exposing the sporangia which split longitudinally to liberate the spores. The outer wall of the spore splits into strips as the spore ripens forming four long elaters which undergo hygroscopic movements. They are spirally coiled round the spore when dry, uncoiled when moist. By this means the spores cling together in groups as they are dispersed.

The spores are all of one size; *Equisetum*, like the fern, is *homosporous*. When the spores fall to the ground and germinate, however, they usually give rise to **prothalli** *of two kinds*. Some of the spores produce prothalli bearing antheridia only; others produce prothalli bearing archegonia only. It is interesting to note that we have an indication of the same thing occasionally in the fern (p. 388). It is the rule in *Equisetum*. The differentiation of sex has been carried back from the sexual organs (antheridia and archegonia) to the structures bearing these sexual organs, so that we may now speak of male and female prothalli.

The prothalli are unisexual, and the gametophyte is represented by two plants. They are more or less lobed structures and *as a rule the male prothalli are much smaller than the female ones.* In other characters they resemble those of the fern, as do also the sexual organs. Fertilisation is effected and an embryo sporophyte developed in much the same way. The life history may be graphically represented as in Fig. 304.

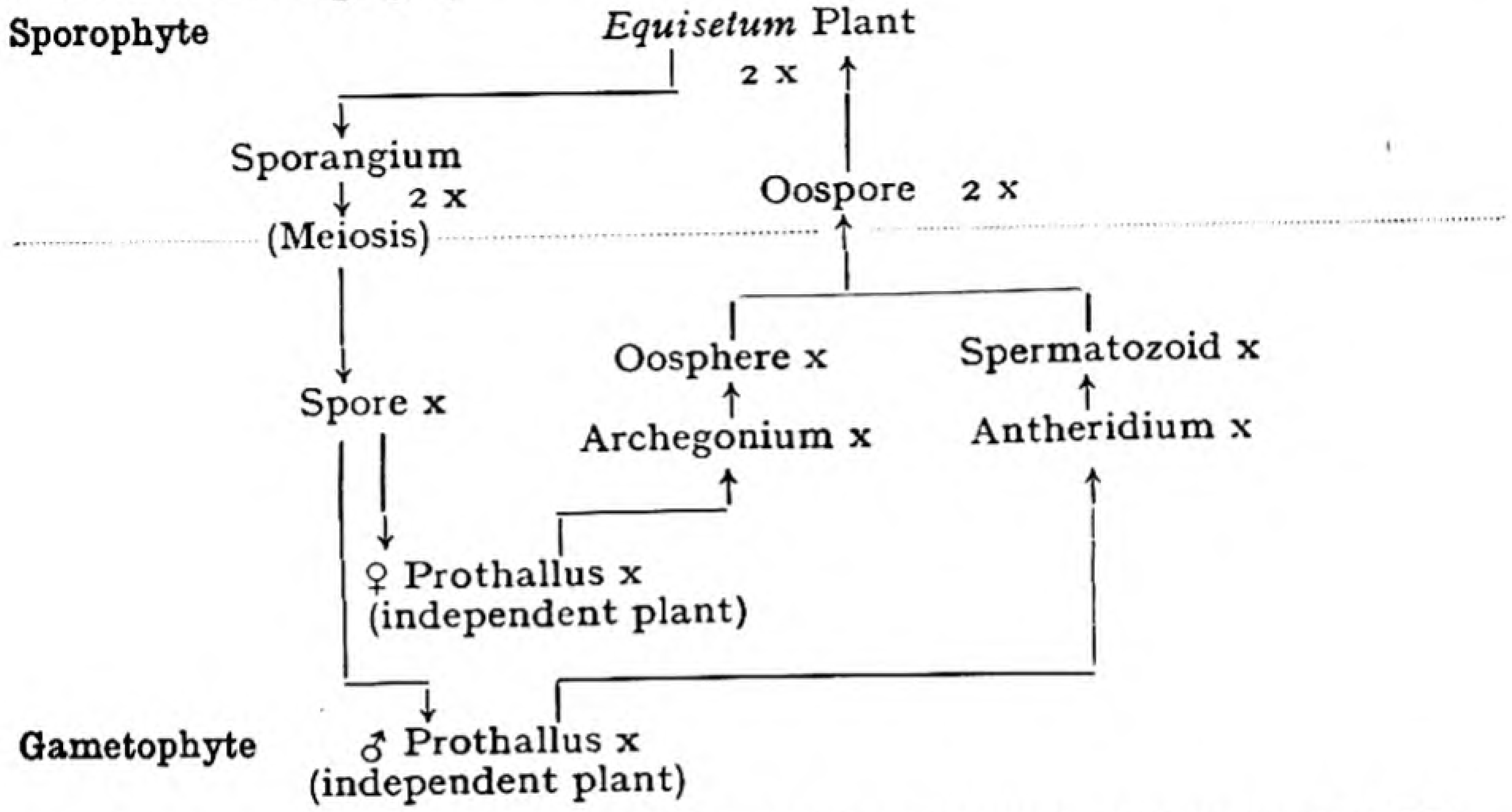
Sporophyte
Equisetum Plant
2 x
Sporangium
2 x
Oospore 2 x
(Meiosis)
Oosphere x
Spermatozoid x
Spore x
Archegonium x
Antheridium x
♀ Prothallus x
(independent plant)
Gametophyte
♂ Prothallus x
(independent plant)

Fig. 304. LIFE HISTORY OF *Equisetum*, GRAPHICALLY REPRESENTED. (x = the haploid number of chromosomes.)

C. SELAGINELLA

25. General Characters (Fig. 305)

The plant is the sporophyte. The external vegetative characters vary considerably in the different species, which number over three hundred and are mainly tropical, only one being a native of Britain —namely, *S. spinosa*. Many species are small, moss-like plants, with creeping stem and dorsiventral symmetry. Others are larger, and more or less erect and isobilateral. In the single British species, while the main stem is creeping, the *branches* are erect and have radial symmetry. Some tropical species are climbing plants, often growing to a great height.

The slender **stem** usually bears four rows of leaves—two rows of small dorsal leaves on the upper surface, two of larger ventral leaves at the sides of the stem. The arrangement of the leaves appears at first sight to be opposite and decussate, one large and one small leaf apparently arising at each node. The leaves, however, are somewhat twisted, and close examination shows that each leaf arises from its own node, the dorsal leaf being slightly above the opposite ventral one. In the single British species all the leaves are of the same size and the spiral arrangement is immediately obvious. In all the species a small membranous **ligule** is developed on the upper surface of the leaf at its base.

The **branches** are developed from lateral buds which do not arise in the axil of a leaf but above one of the ventral leaves. Since they develop almost as rapidly and as strongly as the main stem, the branching assumes a dichotomous appearance; it is false dichotomy, and the branches all lie in one plane.

The **roots** in some species are developed adventitiously on the stem; in other species they are borne on peculiar specialised branches, called **rhizophores.** These organs are intermediate in structure and development between roots and stems. Like stems, they have no root-cap, and are developed exogenously; they resemble true roots in internal structure and in the fact that they bear no leaves or reproductive organs.

The rhizophores, when present, are given off usually from the lower (ventral) surface of the stem, one from below each point where an ordinary branch arises. They grow down to the surface of the soil without branching, but on reaching the soil give rise, by endogenous development, to a number of true roots.

The **reproductive organs** (Figs. 305 and 307), are produced at certain periods towards the apices of fertile or reproductive shoots. These reproductive shoots are more or less *erect*, and, in nearly all the species, bear spirally arranged sporophylls, which do not differ very markedly from the ordinary foliage leaves.

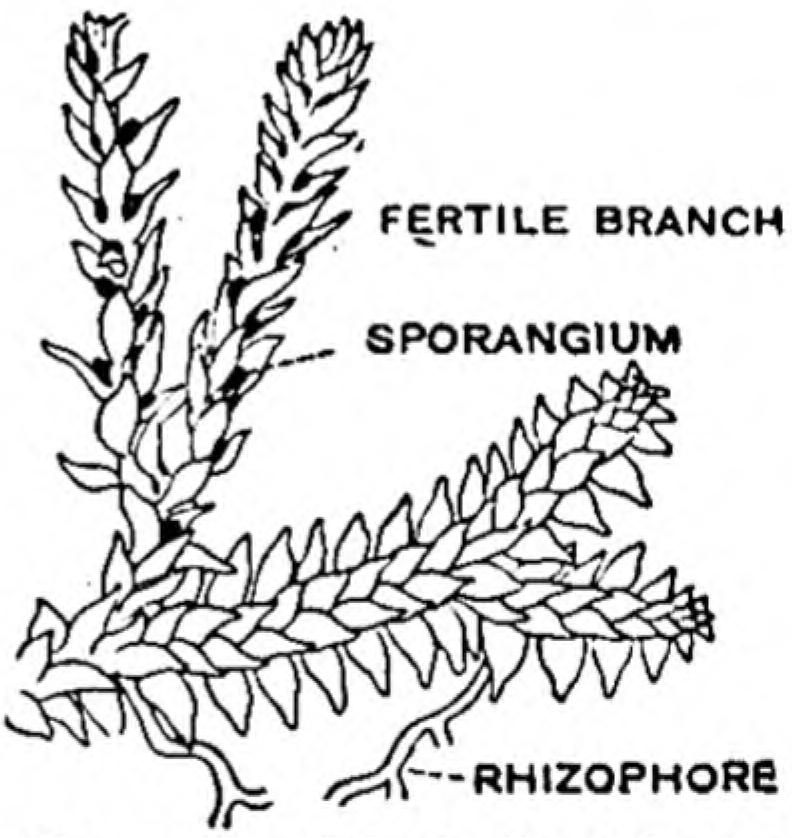

Fig. 305. *Selaginella helvetica.*

The reproductive bodies are **spores** borne in **sporangia.** The sporangia are of two kinds, **megasporangia** and **microsporangia,** each of the former containing usually four large **megaspores,** each of the latter a large number of small **microspores.** Thus *Selaginella* is *heterosporous.* The same cone usually bears both kinds, the microsporangia in the upper region, the megasporangia in the lower, although this is not always the case, for the megasporangia may occur in the middle of the spike. Each sporangium has a short stalk and a rounded capsule.

Vegetative reproduction (by tuber-like structures) occurs in two Indian species, *S. chrysocaulos* and *S. chrysorrhizos.*

26. Stem (Fig. 306)

Some species of *Selaginella* have a small-celled primary meristem, others have a two-sided apical cell. In most species the stem has two or three steles. Each stele is suspended in the middle of a large air-space by a number of delicate trabeculae, which may represent the stretched endodermis, but all trabeculae are not endodermal. In *S. Martensii* the trabeculae cells have a thickening band about their middle, characteristic of an endodermis. The stele is concentric. The central **xylem** consists of slender scalariform tracheides.

According to the species one, two, or a number of **protoxylem** groups can be distinguished.

In *S. spinosa* the protostele of the lower part of the stem has a single central protoxylem, *i.e.* it is *endarch* and *monarch*; but, higher up, the protoxylem divides into from three to eight groups, which pass to the periphery of the xylem so that the stele becomes *exarch* and *polyarch*. In *S. Martensii* it is diarch. This exarch arrangement of xylem *in stems* is found only in the group of Vascular Cryptogams to which *Selaginella* belongs.

The **phloem** consists of thin-walled sieve-tubes with lateral sieve-plates. Outside the phloem is a **pericycle**, consisting of two or three layers of parenchyma. The pericycle, however, in *Selaginella* is derived from the same layer of ground-tissue as the endodermis. There is no secondary growth.

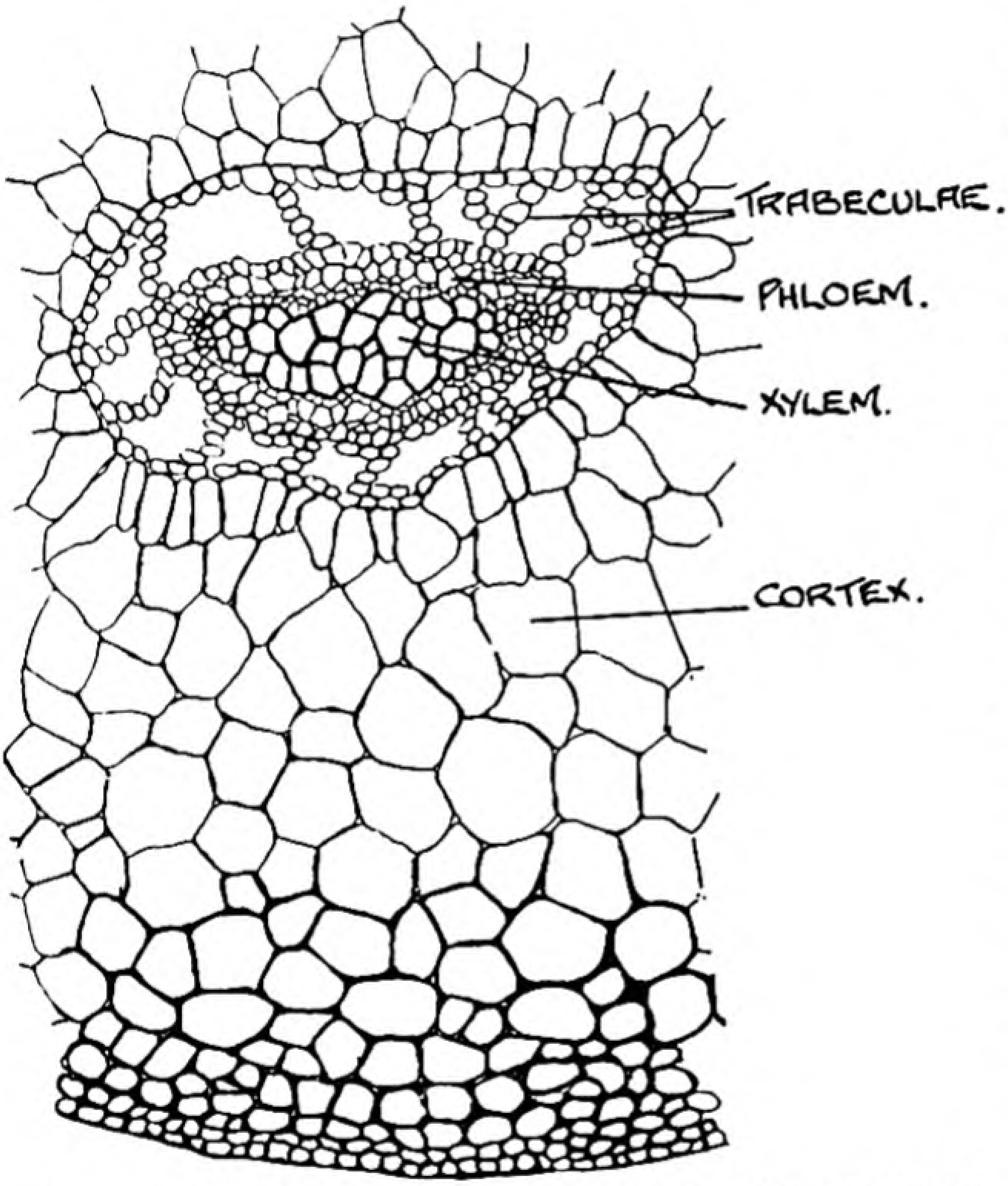

Fig. 306. *Selaginella Martensii.* TRANSVERSE SECTION, STEM.

The **ground-tissue** of the stem consists of comparatively thin-walled, more or less elongated cells, without intercellular spaces (prosenchyma).

The **epidermis** also consists of elongated pointed cells, and has no stomata.

27. Leaf

The leaf is entire, and has a very simple structure. Each of the epidermal cells contains a few relatively large chloroplasts. Stomata are usually confined to the lower surface. The mesophyll is not clearly differentiated into palisade and spongy layers. A single vascular strand runs through it. This strand is concentric. The central xylem is surrounded by a layer of phloem, outside which is an endodermis. In some species longitudinal air-spaces are found in the mesophyll.

28. Rhizophore and Root

These are both protostelic, and agree in internal structure. The stele is monarch. The root grows by a single apical cell; the rhizophore may have a single cell, according to the species, like the stem.

29. Sporangia and Spores (Figs. 307 and 308)

The sporangium consists of a capsule borne on a short, stout stalk. The wall of the capsule consists of two layers of cells, and has no annulus. The megasporangium is somewhat larger than the microsporangium. The spores as usual have two coats, the outer being cuticularised. A large amount of food substance is stored inside the megaspore, consisting chiefly of oil.

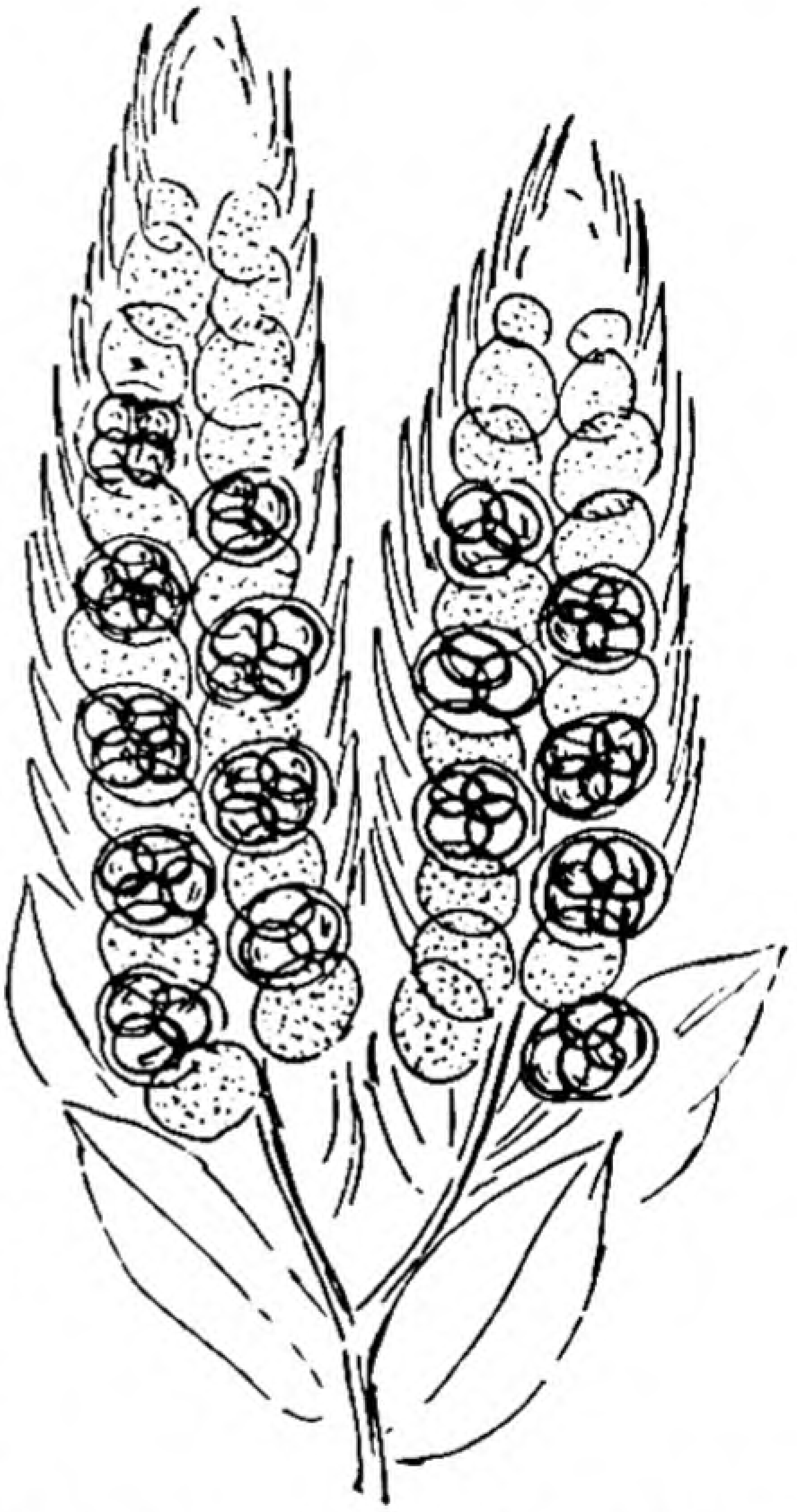

Fig. 307. *Selaginella*: Fertile Shoot showing distribution of Micro- and Mega-sporangia.

30. Development of Sporangium

The sporangium arises from a group of meristematic cells at the stem apex, either on the stem immediately above the primordium of the sporophyll, or on the surface of the sporophyll. It is therefore not axillary although it may appear so in the mature plant. The outermost layer forms the wall of the sporangium. Beneath this, at an early stage, can be recognised a row of large cells which is the *archesporium*. This archesporium gives rise to a group of sporogenous cells surrounded by a layer of *tapetal cells*. The sporogenous cells give rise to spore-mother-cells, as in the fern.

So far the development of both mega- and micro-sporangia is the same, but from this point differences are observed. In the microsporangium the spore-mother-cells separate from each other and float freely in a nutritive fluid formed by the disorganisation of the tapetal cells. Then each spore-mother-cell divides meiotically to give rise to four microspores, as in the fern. The microspores are tetrahedrally arranged, that is, one at each of the four corners of a tetrahedron or triangular pyramid. In the megasporangium only one of the spore-mother-cells increases in size, and produces four megaspores in the same way as a mother-cell produces microspores. The other spore-mother-cells are disorganised and serve, along with the tapetum, as nourishment to the developing megaspores.

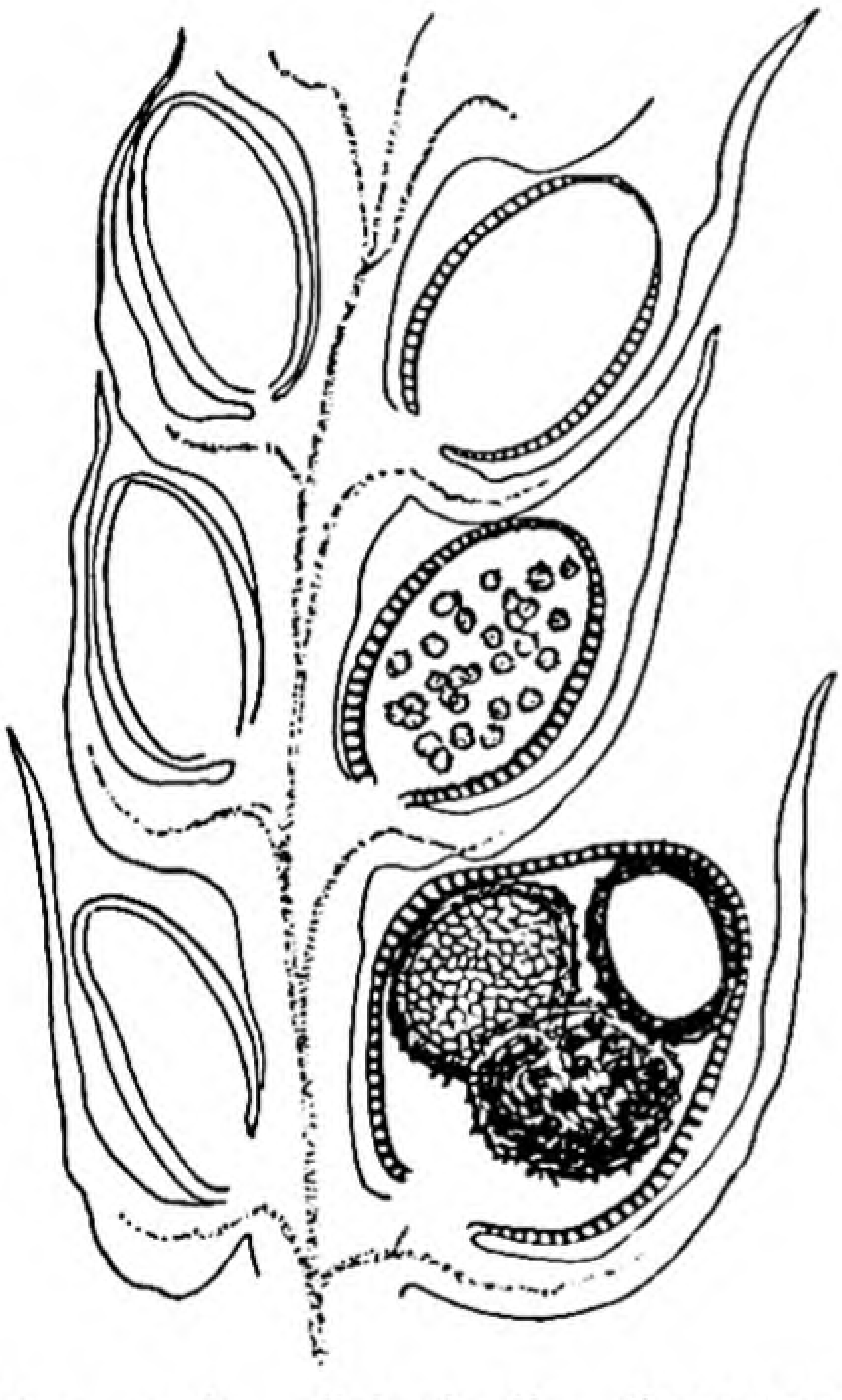

Fig. 308. *Selaginella*, Longitudinal Section. Cone showing Mature Micro- and Megasporangia.

The wall of the sporangium is double, but one layer of tapetal cells persists, so that the wall seems to consist of three layers. Dehiscence of the sporangium takes place on drying and the spores are liberated. There is no annulus, but the contraction resulting from drying produces a transverse slit which opens wider so as to expose the spores.

31. Germination of the Spores—Prothalli and Sexual Organs

The *germination of the megaspore begins before it is set free from the sporangium.* The nucleus of the spore divides into two. One daughter-nucleus passes to the apex or pointed region of the spore, the other to the basal region.

A process of cell-division then begins. It is most active in the apical region, and there results in the production of a small-celled tissue. In the lower region the process is much less active, and actual cell-formation may not take place there till after the spore has fallen to the ground. The cells formed in this region are larger and filled with food-material. The megaspore ruptures at the apex by a tri-radiate fissure which exposes the small-celled tissue immediately underneath. On this an **archegonium** is developed, and others are formed later if fertilisation is not effected.

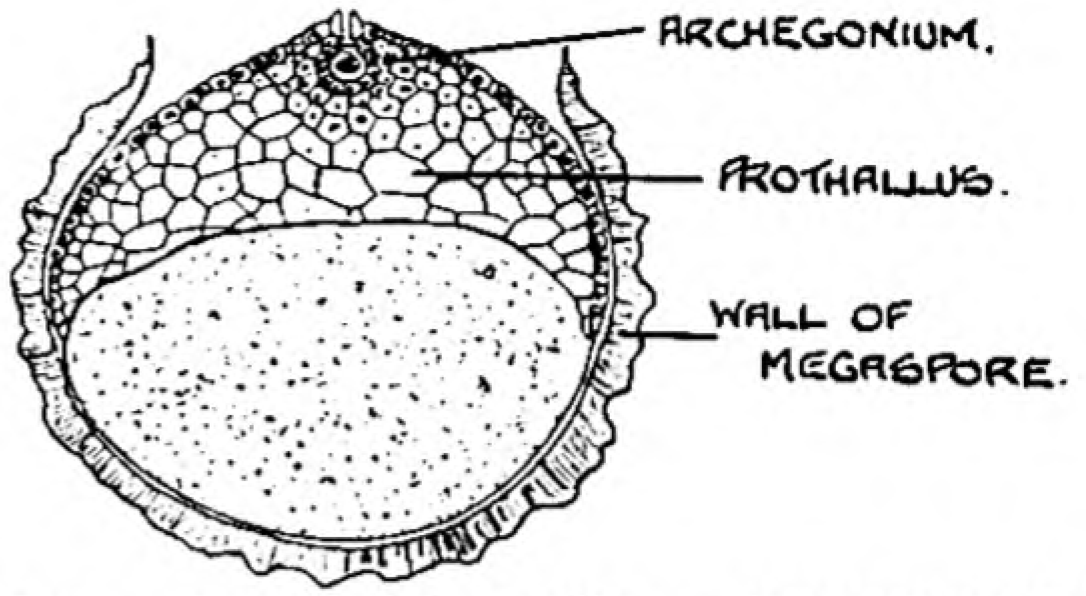

Fig. 309. *Selaginella.* LONGITUDINAL SECTION OF GERMINATED MEGASPORE SHOWING ONE ARCHEGONIUM IN THE EXPOSED PROTHALLUS.

It is evident that the tissue formed in the megaspore is the **female prothallus** (Fig. 309). It protrudes slightly, turns green in the presence of light, and may even develop one or two rhizoids, but it is not set free from the spore as an independent plant, like the prothallus of the fern or of *Equisetum*. It is nourished by the food-material stored in the spore. This reduction of the female prothallus to a minute and almost dependent structure should be carefully noticed.

The structure and development of the archegonium (Fig. 310) are almost the same as in the fern. The difference is that the neck is shorter, consisting of only eight cells; each of the four longitudinal rows of the neck consists of two cells.

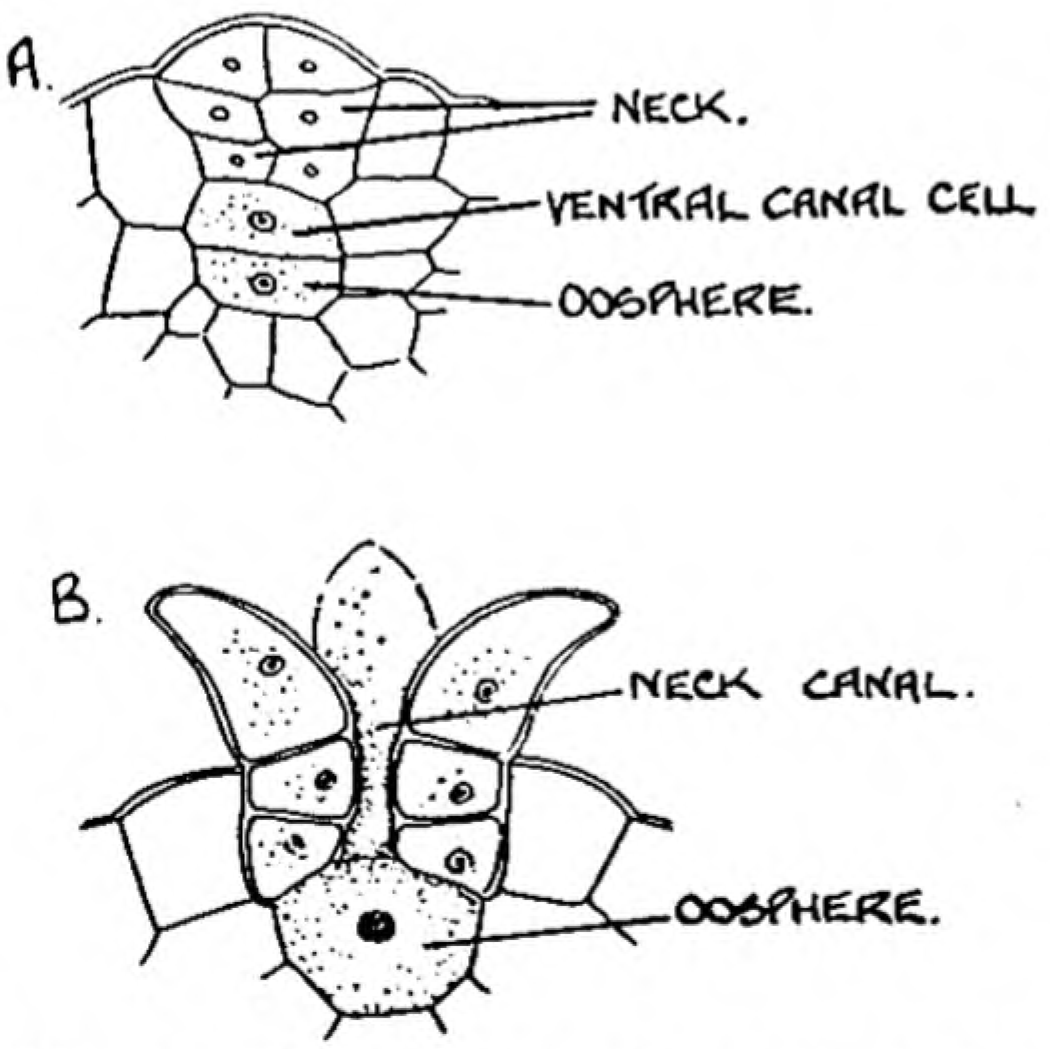

Fig. 310. LONGITUDINAL SECTION, ARCHEGONIUM OF *Selaginella*.
A, Younger stage; B, Older stage.

The microspores also begin to germinate before they are set free. The microspore increases in size, and a small cell is cut off at the pointed end. Then the rest of the spore divides into ten or twelve cells, eight peripheral cells surrounding either two or four central cells (according to the species). The *central* cells undergo further division, and the small cells thus produced are the mother-cells of spermatozoids (Fig. 311). In each a *biciliate* spermatozoid is formed in exactly the same way as in the fern.

The small cell first cut off represents an extremely rudimentary **male prothallus,** and may be called the *prothallus-cell.* The eight peripheral cells represent the wall of an **antheridium,** inside which the spermatozoids are produced. The extreme reduction of the male prothallus is of great interest, and is correlated with the small size of the microspore.

During the course of development the spore-wall is ruptured. Later the peripheral cells undergo disorganisation and nourish the spermatozoid mother-cells. Eventually the spermatozoids are set free.

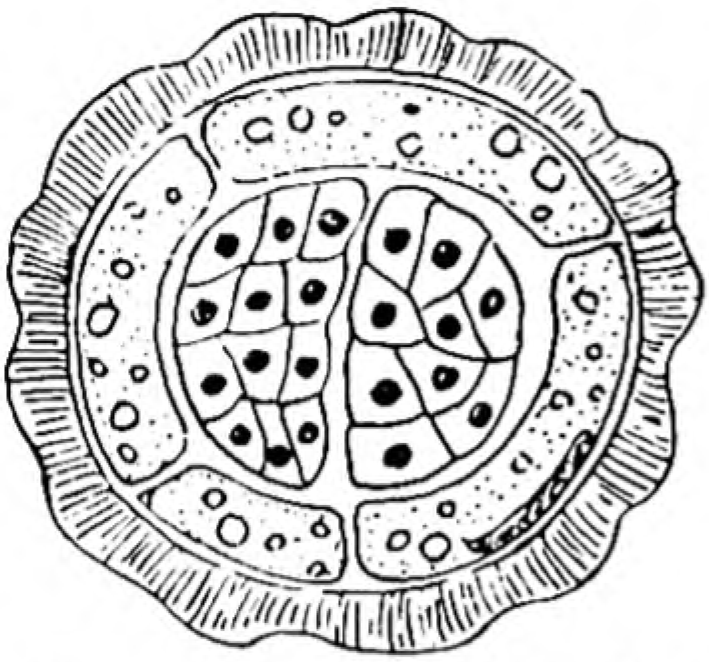

Fig. 311. SELAGINELLA. GERMINATION OF MICROSPORE.

32. Fertilisation and Development of the Embryo (Figs. 309, 312, and 313)

The process of fertilisation is essentially the same as in the fern and *Equisetum.* A spermatozoid enters the ovum and the two nuclei fuse. The **oospore** which is thus formed segments and develops into an embryo sporophyte.

The first dividing wall is at right angles to the axis of the archegonium. It divides the oospore into upper and lower cells. The upper cell either remains unicellular or undergoes only a few divisions, the resulting structure being called the **suspensor.** The function of the suspensor is to push the developing embryo down into the tissue of the prothallus; there is no structure corresponding to it in the fern.

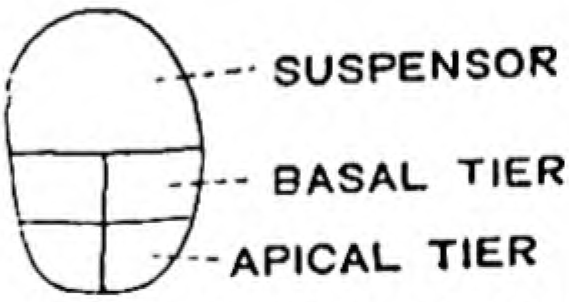

Fig. 312. SEGMENTATION OF OOSPORE OF *Selaginella.*

(Diagrammatic.)

The segmentation of the lower or *embryonic* cell is comparable to that of the whole oospore in the fern. It is divided by basal, quadrant, and octant walls, formed somewhat irregularly, into eight cells (octants) forming apical (or epibasal) and basal (hypobasal) tiers of four cells each. From the apical tier are formed the stem-apex and the two cotyledons; the hypobasal tier gives rise to the hypocotyl. In some species (not in *S. spinosa*) the hypocotyl becomes enlarged and forms a massive haustorium or absorbing organ known as the **foot** or " feeder." The first root is adventitious and is developed from the hypocotyl close to the suspensor.

The development of the embryo in *Selaginella* should be carefully compared with that of the fern (p. 388), and also with that of the Angiosperm (p. 268).

The developing embryo grows down into the lower part of the prothallus from which the foot absorbs food material. Eventually the stem and cotyledons escape from the spore and grow above ground, while the first and other adventitious roots pass down into the soil.

33. Life History

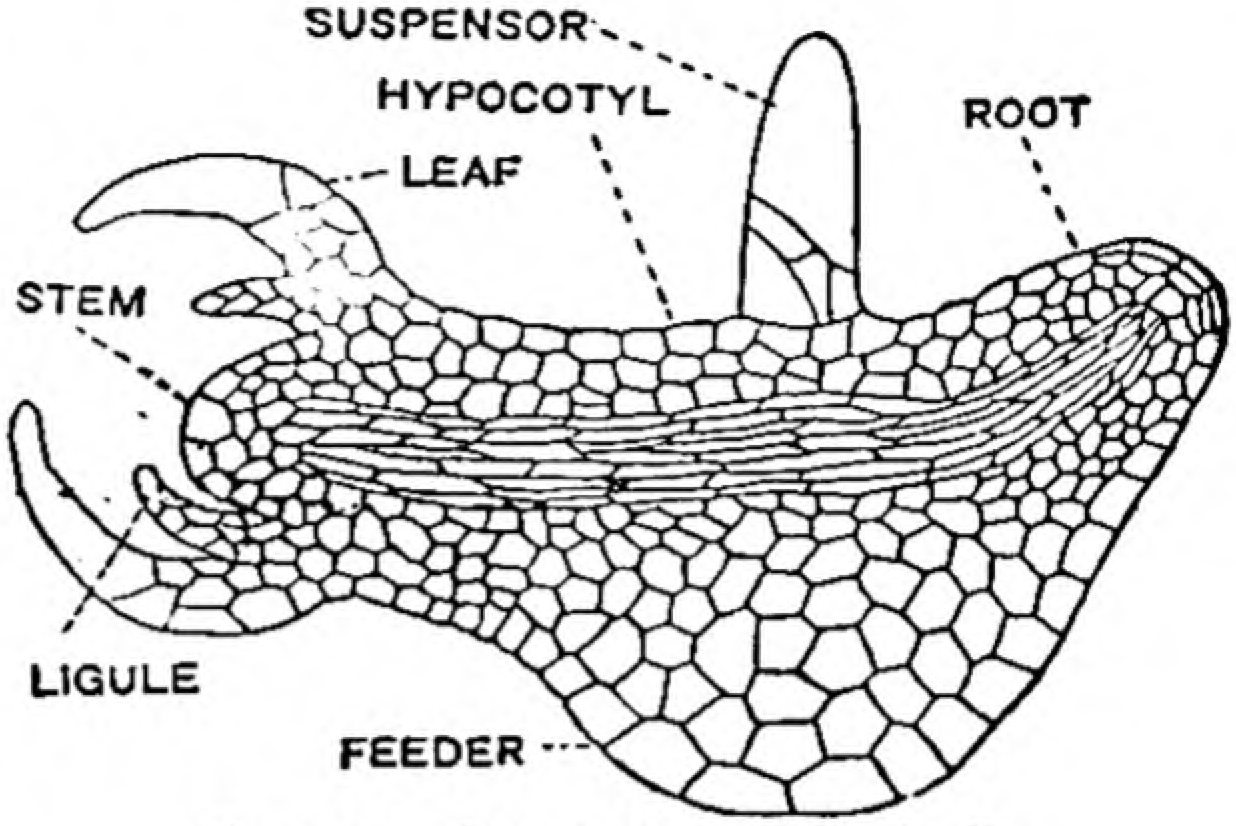
SUSPENSOR
HYPOCOTYL
ROOT
LEAF
STEM
LIGULE
FEEDER

Fig. 313. EMBRYO OF *Selaginella*. (Longitudinal section.)

The life history may be graphically represented as in Fig. 314. The following important points should be noticed. In the first place the differentiation of sex has been carried back another stage. There are not only two kinds of prothalli, as in *Equisetum*, but these prothalli are developed from spores of quite different appearance, that is, *Selaginella* is heterosporous. In the second place, the *reduction* of the male and female prothalli, *i.e.* the gametophyte, has to be noticed. In *Selaginella* the gametophyte, and consequently also the young sporophyte, are nourished mainly by the parent sporophyte. In other words the gametophyte is not a strictly independent organism.

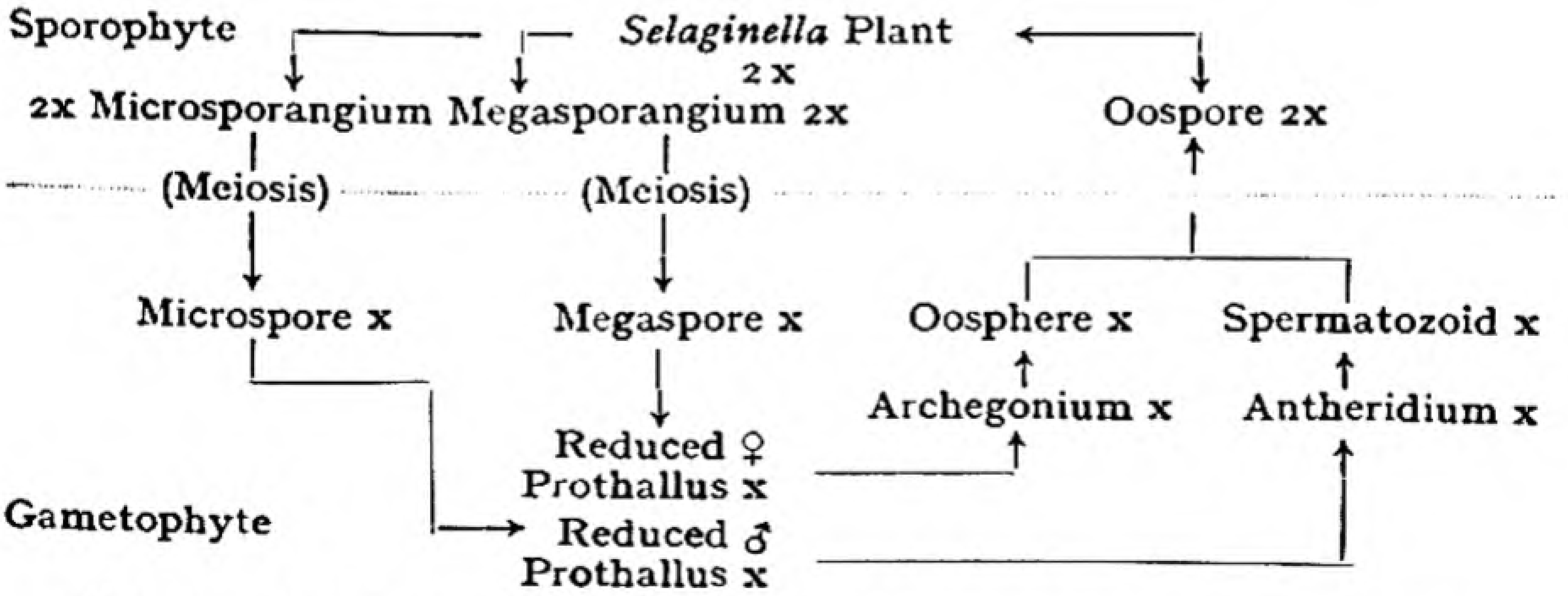
Sporophyte
Selaginella Plant 2x
2x Microsporangium
Megasporangium 2x
Oospore 2x
(Meiosis)
(Meiosis)
Microspore x
Megaspore x
Oosphere x
Spermatozoid x
Archegonium x
Antheridium x
Reduced ♀ Prothallus x
Gametophyte
Reduced ♂ Prothallus x

Fig. 314. LIFE HISTORY OF *Selaginella* GRAPHICALLY REPRESENTED. (x = the haploid number of chromosomes.)

Fertilisation of the megaspore may take place within the sporangium, and in one species of *Selaginella* it has been recorded that the young sporophyte actually develops on the parent sporophyte.

The life histories of fern, *Equisetum* and *Selaginella* should be carefully compared. While there are many differences, by reason of which these three types are placed in different classes of the Vascular Cryptogams, the *general* course of the life history is similar. In all three there is a more or less distinct alternation of generations, and equivalent or *homologous* structures occur at the same points in the life history. The graphical life histories which have been given will make clear the more important homologies.

D. LYCOPODIUM

34. General Characters

The genus *Lycopodium* (club-moss), including about 100 species, belongs to the same class of Pteridophyta as *Selaginella*. Most of the species are small plants, but some attain a height of 4 or 5 feet; many tropical species are epiphytic. The British species are all found in hilly districts and exhibit marked xerophytic characters.

The plant (Fig. 315) is the sporophyte. In its general appearance it resembles *Selaginella*. The firm slender stems, which may be either erect (*L. Selago*) or trailing (*L. clavatum*), are completely covered with small stiff leaves, usually arranged spirally. The leaves have *no ligule*. In some species the branching of the stem is dichotomous; in others it is really lateral although it resembles dichotomy. The roots are adventitious and dichotomously branched.

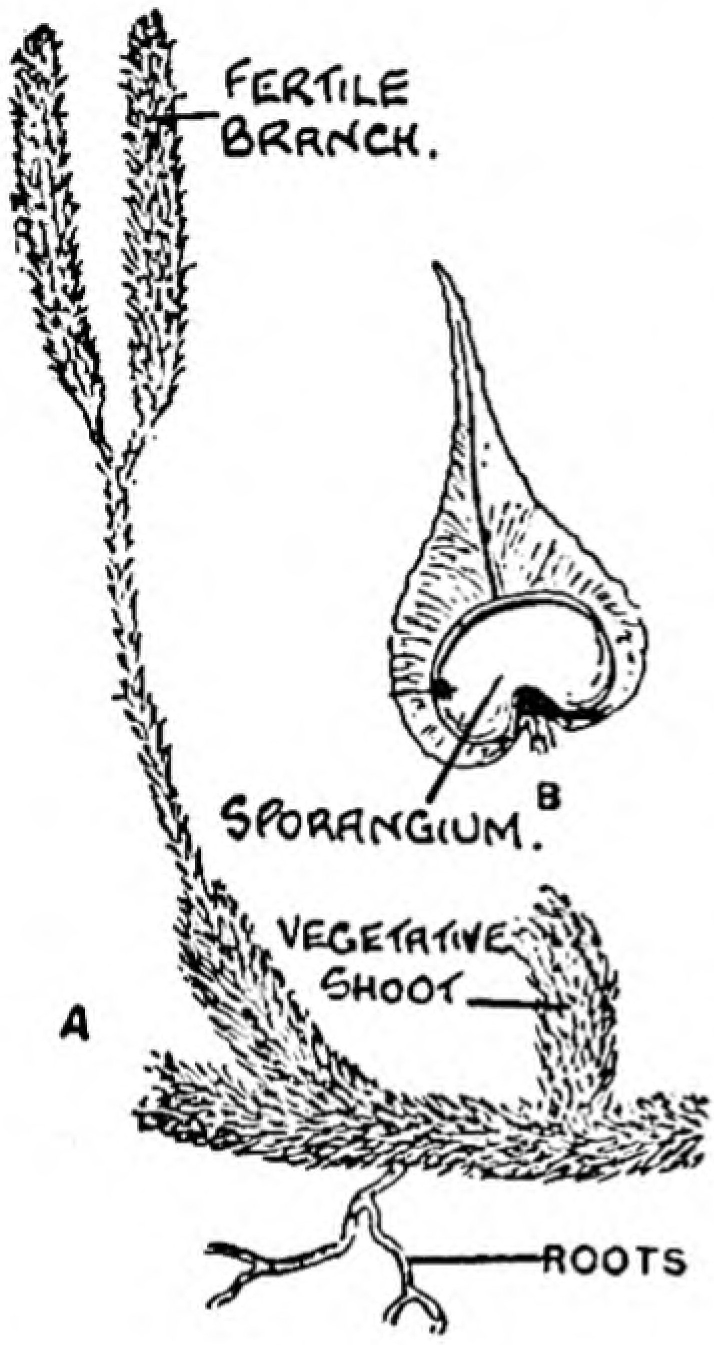

Fig. 315.

A, Part of *Lycopodium clavatum*, showing stem, leaves, roots, and sporangiferous spikes; B, A sporophyll and sporangium in surface view.

In the stem there is a central *cauline* vascular cylinder (protostele). The arrangement of vascular tissue differs in different species, but usually there are a number of rays or plates of xylem with intervening or interpenetrating rays or plates of phloem (Fig. 316). The protoxylem and protophloem, as in *Selaginella*, are external (exarch arrangement). There is conjunctive tissue between the xylem and phloem, and the whole vascular cylinder is surrounded by a pericycle and endodermis. The vascular cylinder of the root is similar to that of the stem. The leaves have a single median concentric bundle. Root and stem are both developed from a group of apical cells.

Lycopodium Selago reproduces vegetatively by means of bulbils.

35. Sporangia and Spores (Fig. 315)

Lycopodium is *homosporous*. The sporangia are borne singly, not in the axils of the leaves, but on their upper surfaces near the base. In some species, e.g. *L. Selago*, the stems show alternating barren and fertile regions; the sporophylls are not aggregated or specialised in any way and resemble the sterile leaves. In other species, e.g. *L. clavatum*, the sporophylls are borne in cones on special branches, and differ in shape from the foliage leaves.

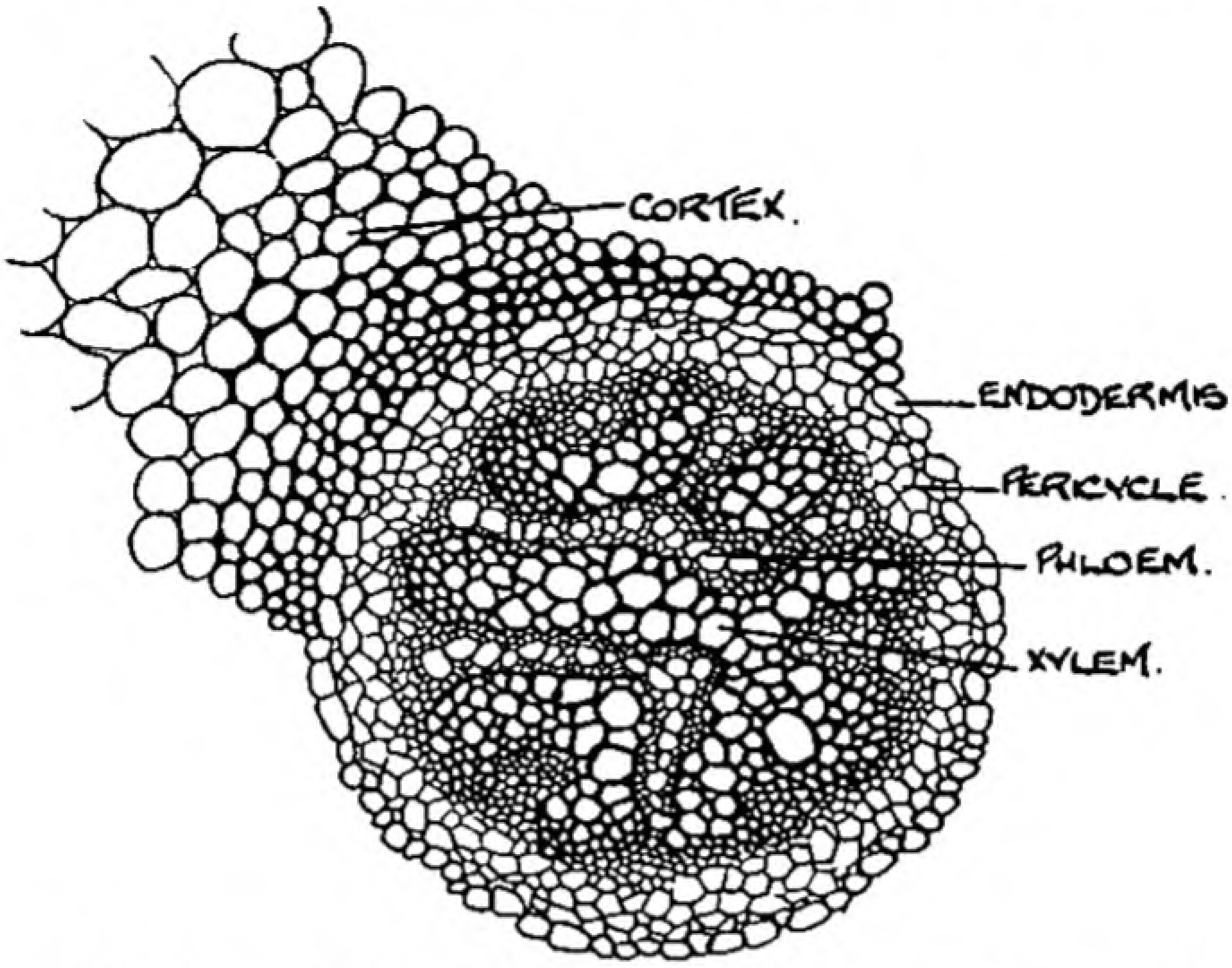

Fig. 316, A. *Lycopodium clavatum.* TRANSVERSE SECTION, STEM.
Detailed drawing.

The sporangium is developed, as in *Selaginella*, from a group of cells, and when ripe contains a large number of small tetrahedral spores.

36. The Gametophyte

The spores on germination produce prothalli which, though small, are the largest and most complex found in the Vascular Cryptogams. In *L. clavatum* and other species they are tuberous, more or less conical, subterranean bodies, which have no chlorophyll and live saprophytically by means of an endophytic (endotrophic) mycorrhiza. In other species (e.g. *L. Selago*) only the lower subterranean part of the prothallus has this character; the upper part reaches the surface of the soil, develops chlorophyll, and becomes more or less lobed. The prothalli are monoecious and bear both archegonia and antheridia similar to those of *Selaginella*.

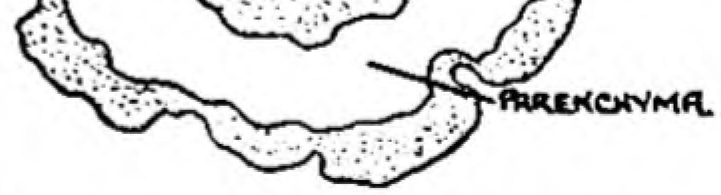

Fig. 316, B. *Lycopodium clavatum.* TRANSVERSE SECTION, STEM.
Diagram.

37. The Embryogeny

The early stages of development are the same as in *Selaginella* (p. 399). The hypobasal tier of cells gives rise to the foot, which may remain small (*L. Selago*), or, if the prothallus is deeply buried, may be strongly developed (*L. clavatum*). From the apical tier of cells are developed the stem, cotyledon, hypocotyl, and first root. In a few species (e.g. *L. clavatum*) there are apparently two cotyledons. The first root is adventitious and in some species developed exogenously.

38. Notes on the Pteridophyta

The Pteridophyta have a well-marked alternation of generations in which the gametophyte, even when growing independently of the sporophyte, is relatively insignificant in size, and undifferentiated into stem and leaf. In the homosporous forms the gametophyte (prothallus) bears antheridia and archegonia, in which the male (spermatozoids) and female (oosphere) gametes are borne. *Equisetum* is exceptional in having spores which are externally similar, but which germinate to produce either male or female prothalli. In the heterosporous forms the gametophyte is reduced, the microspore dividing to produce little more than an enclosed antheridium, whilst the megaspore produces a minute prothallus bearing archegonia. This prothallus arises in the megaspore whilst still within the megasporangium attached to the sporophyll on the parent plant. The megaspore is, however, ultimately liberated, when it opens in order to expose the archegonia to water, so that fertilisation may be effected by motile spermatozoids. By the reduction of the number of megaspores to one, the partial enclosure of the megasporangium by the sporophyll, or by an outgrowth from it, and its retention on the parent plant, we have a possible line of comparison with the simplest seed plants (see Chap. XVI).

CHAPTER XV

THE GYMNOSPERMS

1. Introductory

The Gymnosperms, trees or shrubs, show great variation of form and structure. They extend back to the Palaeozoic period, when they were tall trees with woody, branching stems, bearing simple leaves. Existing plants which show relationship to these fossils are the Cycads, of tropical and sub-tropical regions, but their woody stems are unbranched, and their leaves large and compound. Another plant of interest is *Gingko*, the maiden-hair tree found in the precincts of temples in China and Japan, and possibly owing its present existence to this association. Comparable trees of wider distribution existed in Palaeozoic times.

The Coniferae, mainly natives of temperate regions, represent the most important group of living Gymnosperms. They include evergreen shrubs and trees, with greatly reduced leaves showing xerophytic characters. Many conifers reach the limits of tree vegetation in Arctic and Alpine regions, and the group is represented in the Himalaya, where large forests of firs, spruces, pines, cedars, yews and junipers occur. *Cedrus deodora* is the Himalayan deodár. *Pinus longifolia* (chíl) and *P. excelsa* (kail) are two well-known Indian pines. *P. Gerardiana* occurs in the drier ranges of the Himalaya and Afghanistan, and its seeds form the chilgoya of commerce. *Pinus longifolia* is a three-needled pine and *P. sylvestris* a two-needled one. In their internal structure and life history the various species of *Pinus* agree closely with *P. sylvestris*.

A. PINUS SYLVESTRIS

2. External Characters of Pinus

The full-grown plant is a large tree. Typically it has an elongated **tap-root**; but frequently the lateral roots are strongly developed and the primary root is comparatively short. The main stem is cylindrical and covered with a rugged scaly bark. Secondary growth takes place in the same way as in Dicotyledons, and hence the stem tapers towards the apex.

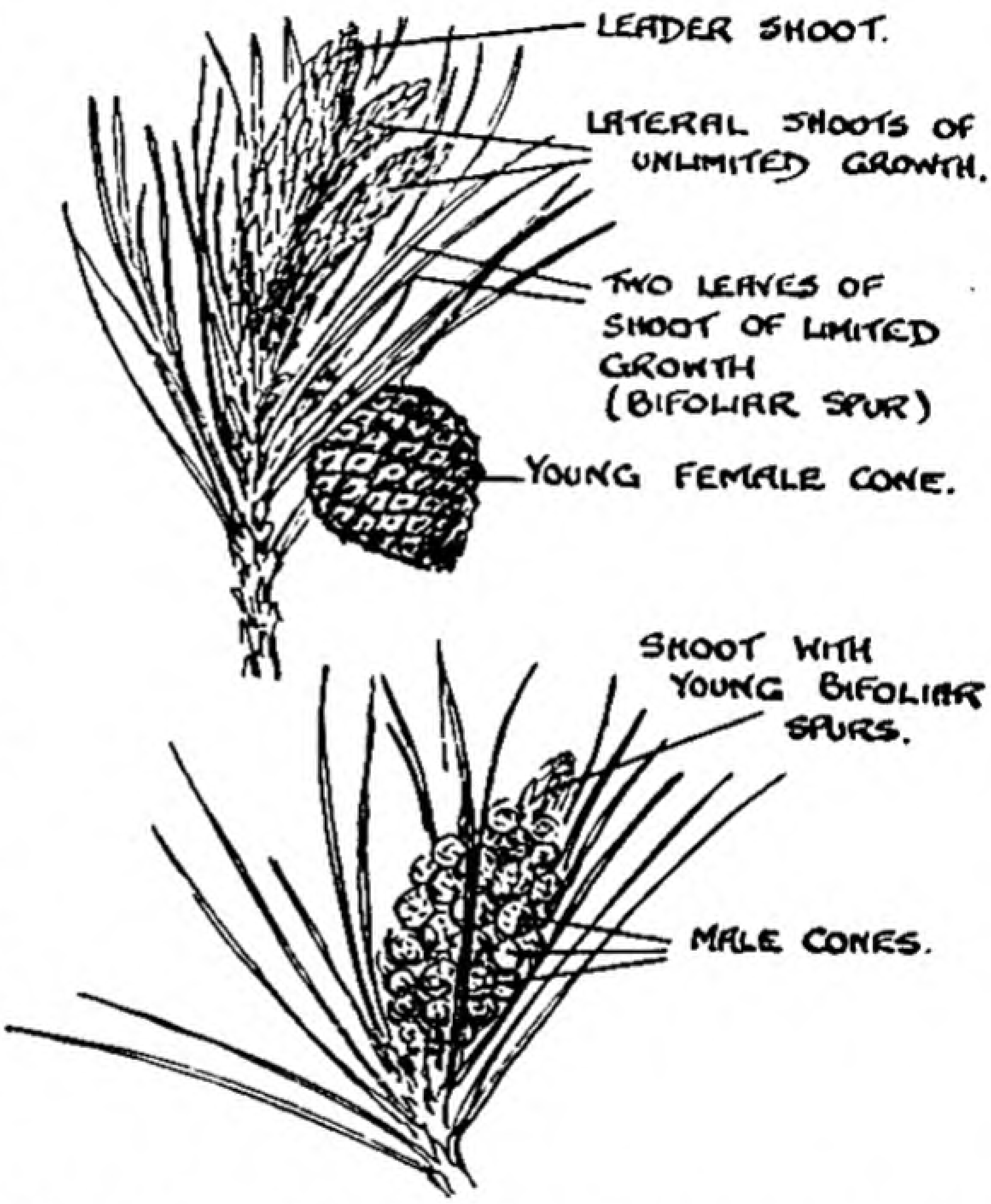
LEADER SHOOT.
LATERAL SHOOTS OF UNLIMITED GROWTH.
TWO LEAVES OF SHOOT OF LIMITED GROWTH (BIFOLIAR SPUR)
YOUNG FEMALE CONE.
SHOOT WITH YOUNG BIFOLIAR SPURS.
MALE CONES.

Fig. 317. BRANCHES OF *Pinus sylvestris*, ABOUT MAY.

The branches grow in apparent whorls from lateral buds developed on each parent axis. These are formed in the axils of scale-leaves, at the end of each year's growth. This regular development of branches gives the tree a very symmetrical appearance, which is, however, frequently spoilt owing to the loss of many of the branches, more especially as the tree grows old. In addition to the ordinary branches, which, as they grow indefinitely, are called *shoots of unlimited growth*, there are numerous **dwarf** shoots or *shoots of limited growth* (Fig. 317). These also arise in the axils of brown scale-leaves borne on the main branches.

The leaves are of two kinds: (*a*) the **scale-leaves** just mentioned, which are the *only* ones borne on the shoots of unlimited growth, and which are also present on the dwarf shoots; (*b*) green **acicular**

foliage leaves ("*needles*"), which occur solely upon the dwarf shoots; they are not borne directly on the shoots of unlimited growth.

The dwarf shoots, with their clusters of green leaves, are called "*spurs.*" The number of green leaves in each cluster varies according to the species of *Pinus*. In *P. sylvestris* there are two, and the dwarf shoots together with their leaves are termed "bifoliar spurs." These persist for a number of years, so that the tree is an evergreen. When they fall off, as they eventually do, it is the dwarf shoots which are shed, and the leaves fall with them.

Pinus has no power of vegetative reproduction.

The presence of a tap-root is characteristic of Gymnosperms. Many, e.g. *Picea*, the spruce, have leaves and shoots of one kind only. The branching is axillary, but buds are not formed in the axils of all the leaves. No buds are formed in the axils of the foliage leaves of *Pinus*, except when the leader has been damaged, e.g. by pine tortrix moth.

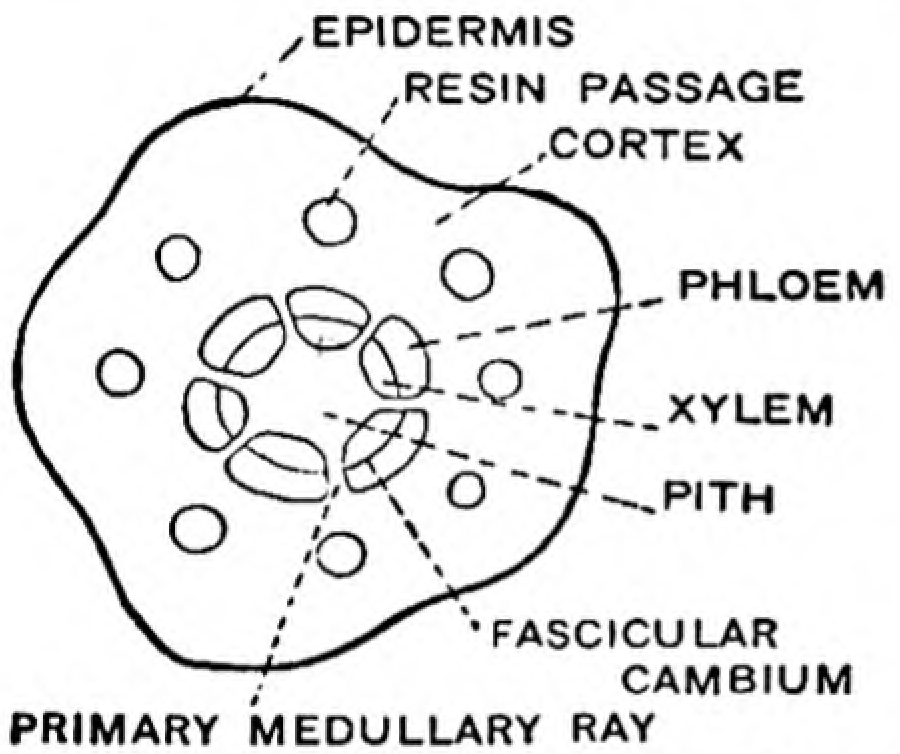

Fig. 318. Young Stem of *Pinus*. (Transverse section: Diagrammatic.)

3. Structure of the Stem

In the general *arrangement* of tissues the stem of the conifer closely resembles that of the Dicotyledon. At the apex there is a small-celled **meristem**, in which, however, there is no dermatogen distinct from periblem; cortex and epidermis originate from a common layer (periblem).

The **bundles** in the primary condition (Fig. 318) are common, collateral, and open, and form a ring in transverse section separated by narrow medullary rays. Within the ring of bundles is the pith, and outside it the cortex. There is no clear distinction between cortex and central cylinder.

Resin-ducts are present in the cortex, each surrounded by a layer of glandular secreting epithelial cells. As the transverse section of the young stem cuts through the bases of the dwarf-shoots its outline is irregular. A somewhat lignified hypodermal layer may be recognised in the outer cortex.

Secondary Growth is effected in exactly the same way as in Dicotyledons (pp. 94 and 121), the cambium ring giving rise to secondary xylem and phloem, and the phellogen to periderm. The phellogen originates in the outer region of the cortex near the surface, though not in the hypodermis, and, later, there is a repeated formation of tangential lines of phellogen cutting off strips of scaly bark (p. 106).

4. The Tissues of the Stem (Figs. 319-321)

There is a close general resemblance to Dicotyledons but considerable differences as to detail. The **xylem** has *no true vessels*, but consists of tracheides with bordered pits. The **protoxylem** consists of annular and spiral tracheides. Small resin-ducts are present in the primary and secondary wood. The **phloem** consists of sieve-tubes and phloem parenchyma; *there are no companion cells.* The sieve-tubes consist of elongated, more or less pointed cells, with sieve-plates on the radial walls.

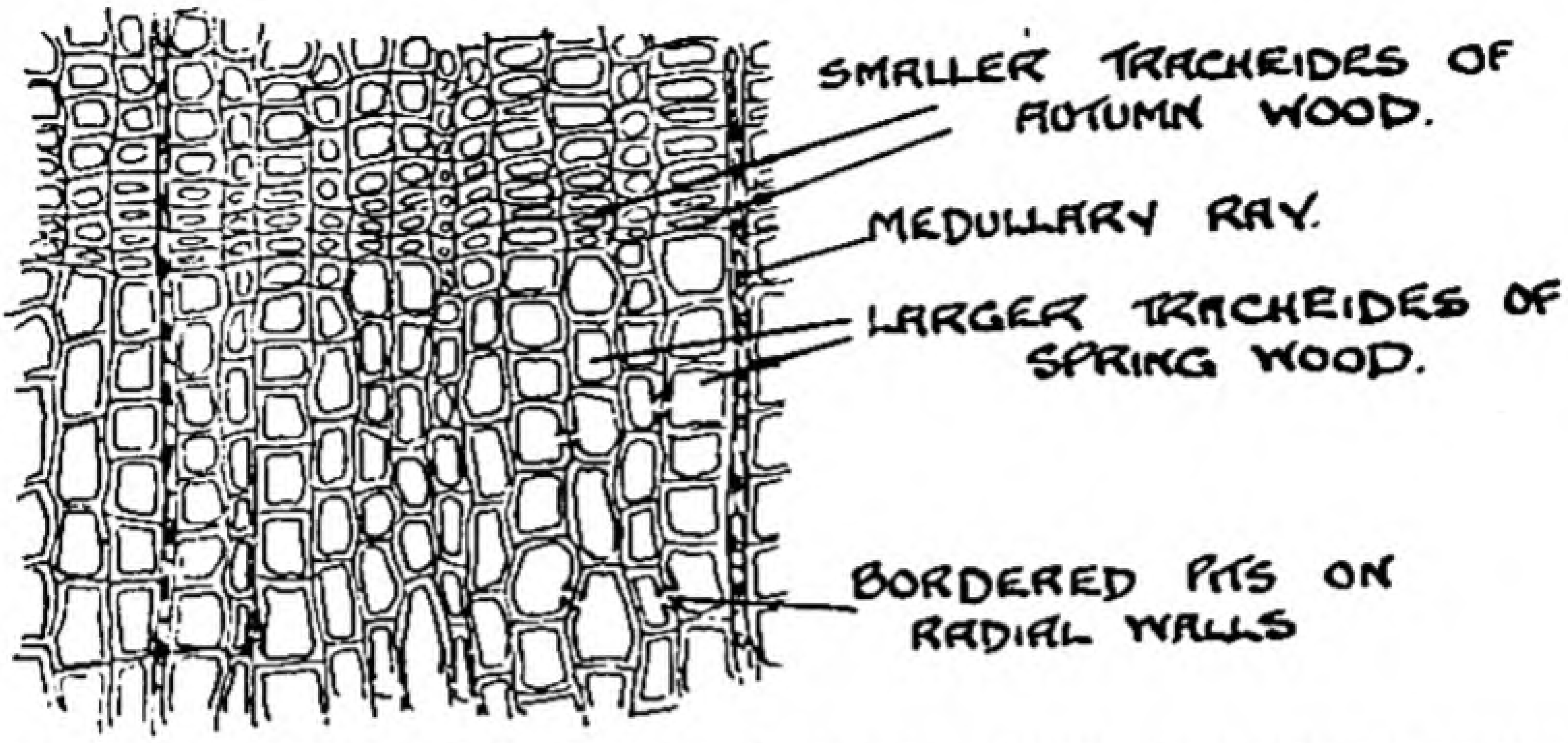
SMALLER TRACHEIDES OF AUTUMN WOOD.
MEDULLARY RAY.
LARGER TRACHEIDES OF SPRING WOOD.
BORDERED PITS ON RADIAL WALLS

Fig. 319. TRANSVERSE SECTION OF STEM OF *Pinus*, SHOWING STRUCTURE OF XYLEM.

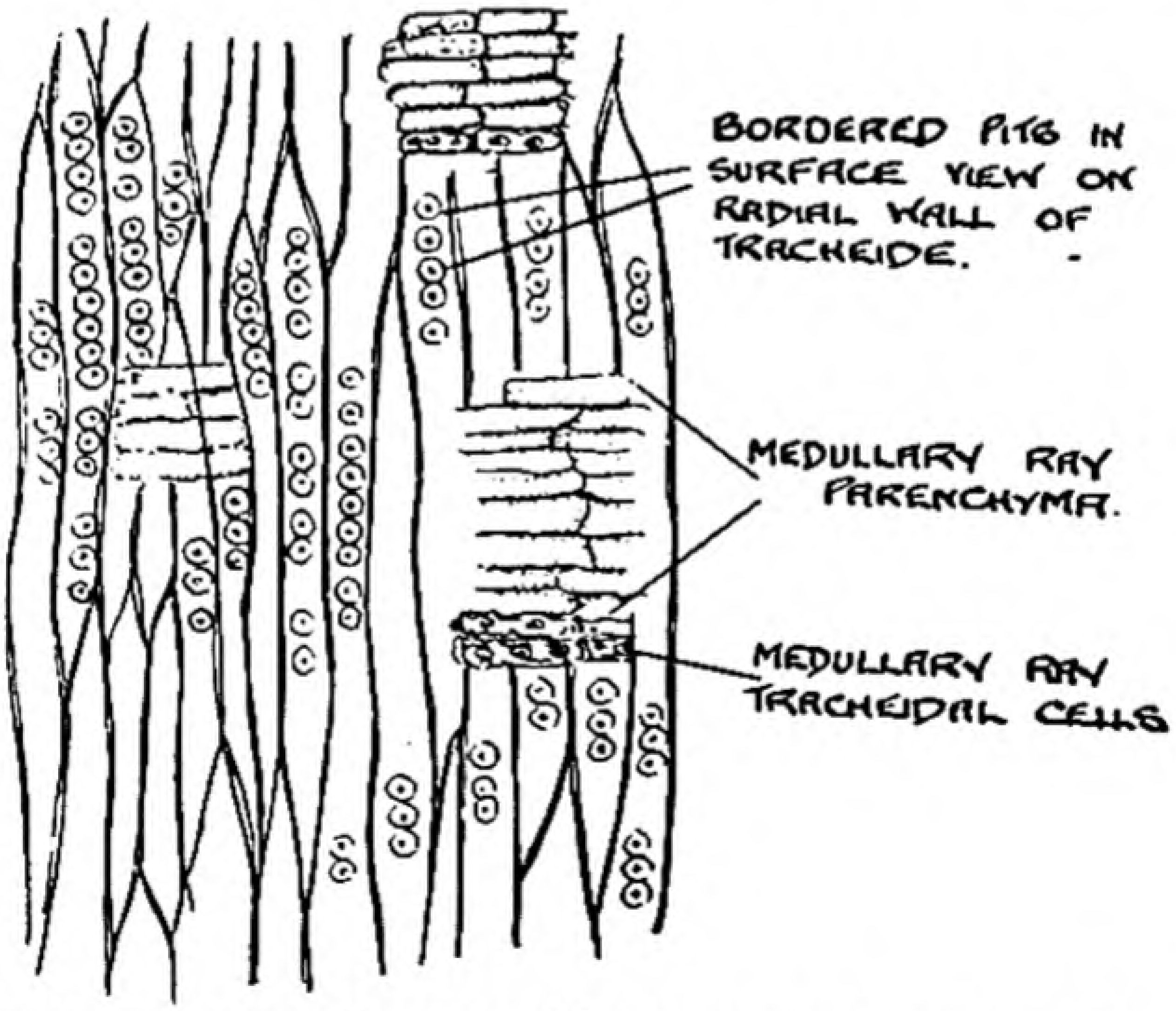
BORDERED PITS IN SURFACE VIEW ON RADIAL WALL OF TRACHEIDE.
MEDULLARY RAY PARENCHYMA.
MEDULLARY RAY TRACHEIDAL CELLS

Fig. 320. LONGITUDINAL SECTION (RADIAL) OF STEM OF *Pinus*, SHOWING STRUCTURE OF XYLEM AND APPEARANCE OF MEDULLARY RAYS.

The structure of the **medullary rays,** however, is more complex than that of Dicotyledons (Figs. 320 and 321). The rays in the secondary wood consist partly of parenchymatous cells containing starch, partly of tracheidal cells elongated radially. These latter allow the radial diffusion of watery fluids since they have bordered pits on their lateral walls, contiguous with those of the tracheides, and on their end walls. In the secondary phloem the rays consist of two kinds of parenchyma, normal medullary ray cells containing starch, and, above and/or below these, albuminous cells usually somewhat elongated vertically. The medullary rays vary in size; the smallest are only two cells high and one cell wide.

Figs. 319-321 show transverse and longitudinal sections of the xylem. A radial longitudinal section runs parallel to the medullary rays in the region in which it is taken, while a tangential longitudinal section cuts *across* them. This will explain the difference in the appearance of the medullary rays in the two sections (Figs. 320 and 321).

The differences in the appearance of the bordered pits are due to the fact that the tracheides are four-sided, two of the sides being approximately radial and two tangential, and that the bordered pits are confined to the radial walls. Thus, in radial section, the radial walls are not cut through and the pits are seen in surface view; while in tangential section the radial walls are cut through and the pits are seen in section (Fig. 321).

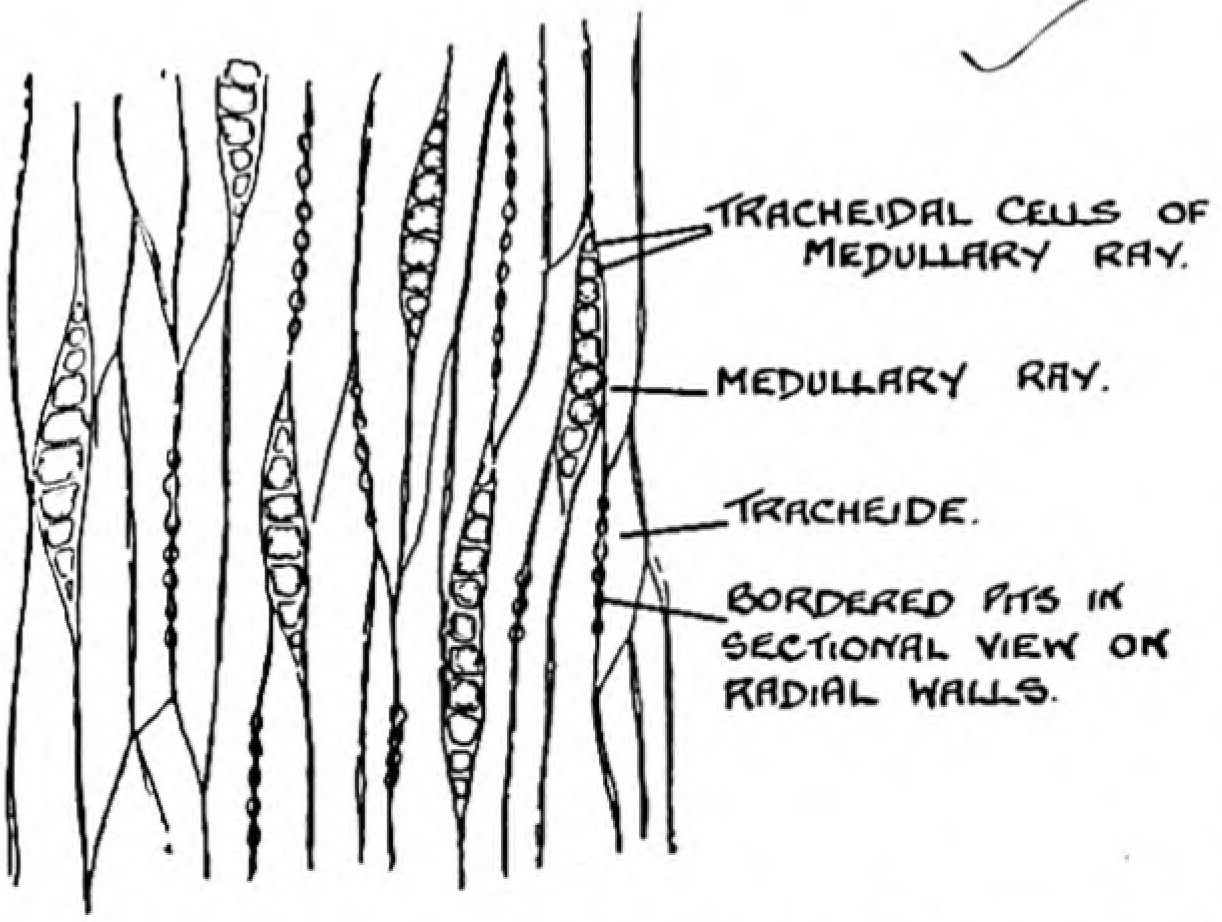
TRACHEIDAL CELLS OF MEDULLARY RAY.
MEDULLARY RAY.
TRACHEIDE.
BORDERED PITS IN SECTIONAL VIEW ON RADIAL WALLS.

Fig. 321. Longitudinal Section (Tangential) of Stem of *Pinus*, showing Structure of Xylem and Appearance of Medullary Rays.

5. The Root

The growth and general arrangement resembles that of Dicotyledons. The apical **meristem** shows periblem and plerome layers, but there is no dermatogen layer, the root-cap and piliferous layer being derived from the periblem. In *Pinus* there are from two to six Y-shaped **xylem** bundles, and an equal number of **phloem** bundles alternating with them; there is a resin-duct between the arms of each Y, and a small pith may be present. This arrangement, however, is not characteristic of conifers as a class. In most cases the stele is diarch (or triarch), and a pith is absent.

In Gymnosperm roots the pericycle consists of several layers, but there is a single-layered endodermis. Secondary growth takes place as in the roots of Dicotyledons. The phellogen originates in the outermost layer of the pericycle. The xylem and phloem have the same structure as in the stem. Lateral roots are developed from the second layer of the pericycle. The roots of *Pinus* have a mycorrhiza, and root-hairs are scantily developed.

6. The Leaf

The tissues of pine leaf as seen in transverse section are represented in Figs. 17, 132 and 322. The **epidermis** consists of extremely thick-walled cells with a strong cuticle. Stomata are developed all over its surface. The guard-cells are sunk beneath the level of the epidermis, so that there is an outer cavity or pit leading down to the pore. Beneath the epidermis there is a sclerenchymatous **hypodermis** interrupted beneath the stomata.

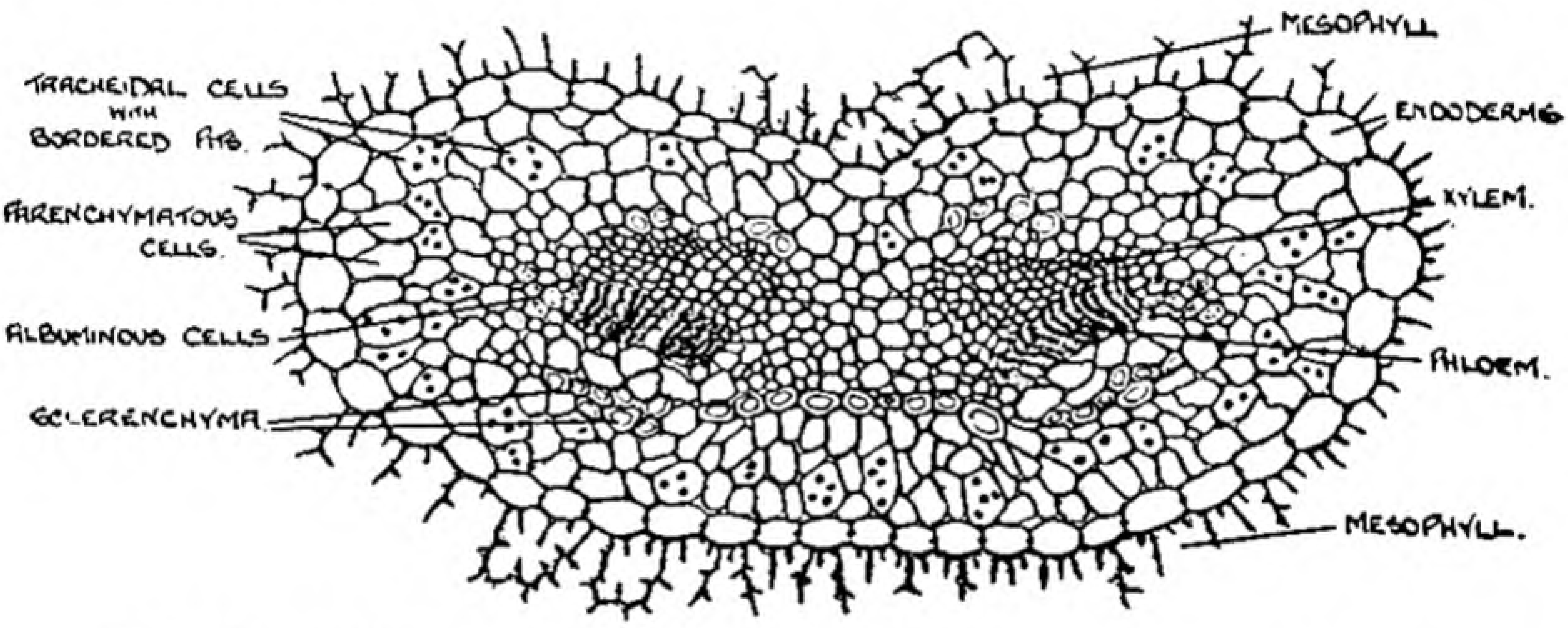

Fig. 322. *Pinus* LEAF. TRANSVERSE SECTION, SHOWING MIDDLE REGION IN DETAIL.

The parenchymatous **mesophyll** is not differentiated into palisade and spongy layers; it consists of thin-walled cells, whose cellulose walls show numerous infoldings. The presence of these appears to compensate for the reduction of leaf surface by increase in the surface area of the individual cells. All parts of the mesophyll are freely aerated by an intercellular-space system best seen in longitudinal sections of the leaf. The cells contain numerous chloroplasts and starch-grains. In the mesophyll, immediately under the hypodermis, are a number of resin-ducts, each with a thin-walled epithelial layer and an investing layer of sclerenchyma. In the middle of the leaf there is a conspicuous **endodermis** surrounding a many-layered pericycle, in which two **vascular bundles** are embedded. The bundles are collateral, the xylem facing the flat upper surface.

In addition to parenchymatous cells containing starch the pericycle includes other parenchymatous cells, rich in protein, called *albuminous cells*, and also lignified cells with bordered pits and no contents, resembling tracheides and called *tracheidal cells*. These two kinds of cells form the **transfusion-tissue** which is characteristic of the leaves of most Gymnosperms. It probably helps in the transference of nutritive solutions, and thus makes up for the poor development of vascular tissue. The tracheidal cells serve for the passage of inorganic solutions from the xylem to the mesophyll; the albuminous cells may collect the elaborated compounds from the mesophyll and pass them on to the phloem. In addition to the transfusion-tissue, sclerenchymatous fibres are found near the bundles.

The narrow acicular form of the leaves, their thick cuticle, the sunken stomata, the presence of a strong hypodermis, and the simple vascular system, are marked xerophytic characters, all tending to reduce transpiration.

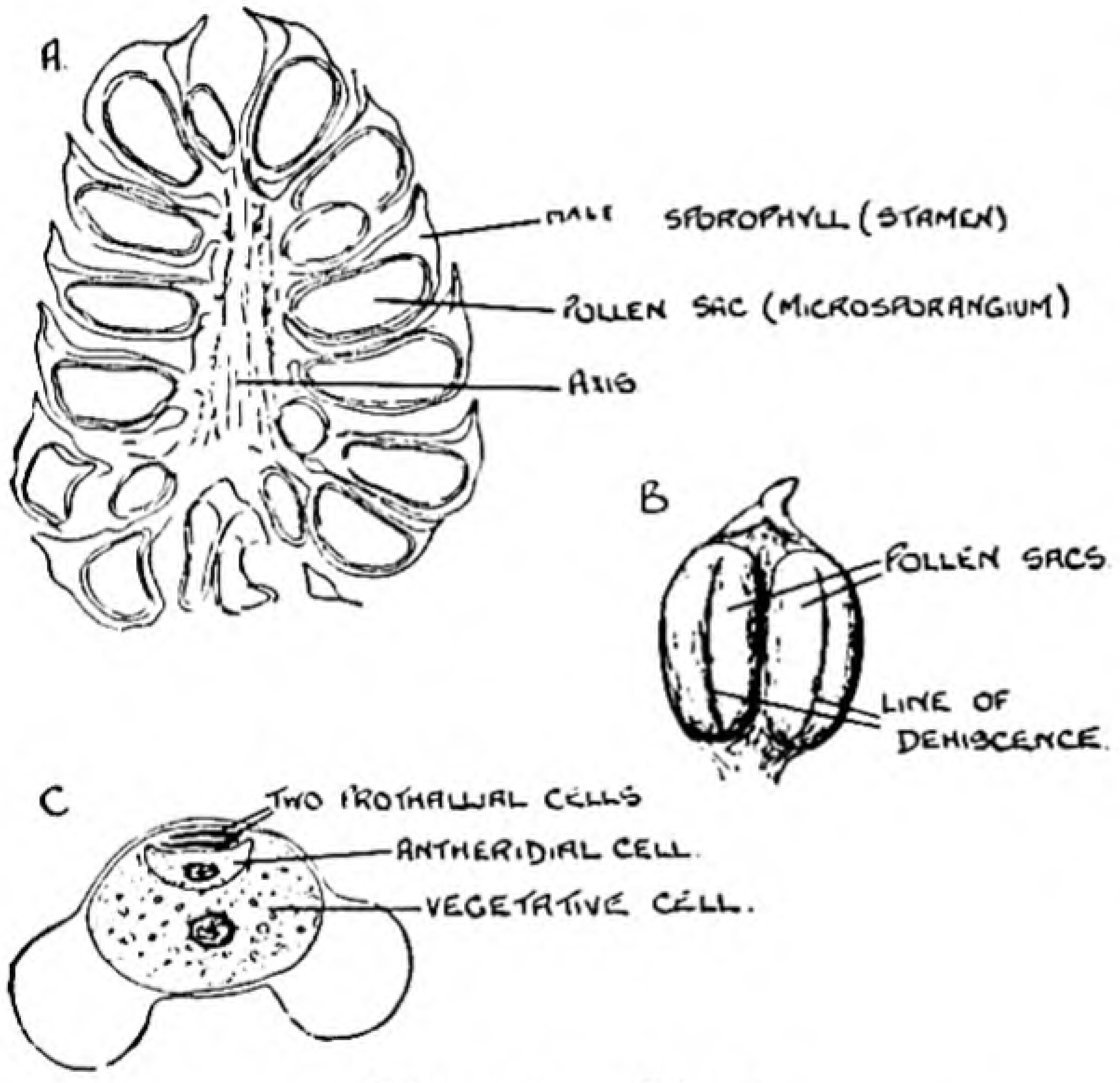

Fig. 323. *Pinus.*

A, Longitudinal section, male cone; B, Male sporophyll—under surface; C, Microspore (pollen-grain) 2-celled stage.

7. The Male Cones
(Figs. 317 and 323)

These appear early in the year—about the beginning or middle of May. They are produced in the axils of scale-leaves at the bases of the developing shoots of the same year, but not on all the shoots. They form a spike at the base of the shoot, and the latter, as it continues to grow, develops ordinary dwarf shoots in the axils of the upper scales. In other words, the male cones are produced at the base of the shoot in place of dwarf shoots.

Each male cone (Fig. 323) consists of a somewhat elongated axis which bears a number of spirally arranged sporophylls. On the under side of each sporophyll two **microsporangia** (pollen-sacs) are developed and these are filled with **microspores** (pollen-grains). The microspores are *at first* unicellular bodies. On each side of the microspore is a small air-sac (Fig. 323, C).

The male cones differ from the flowers of Angiosperms in that (*a*) the axis which corresponds to the receptacle is elongated, (*b*) the male sporophylls (stamens) are less highly differentiated, showing no distinction into filament and anther, (*c*) there are two instead of usually four pollen-sacs. It should also be noticed that the essential organs only are present. There is no perianth, but a few sterile scales occur at the base of the male cone.

Most conifers have male cones like those of *Pinus*. The number of microsporangia, however, differs in different types.

8. The Female Cones
(Figs. 317 and 324)

These are developed laterally in the axils of scale-leaves at the apices of the young elongated shoots. They usually arise from buds laid down near the base of the apical bud on shoots of unlimited growth. There may be from one to four on each shoot.

The female cone, if examined at this early period, is found to be a small, erect, reddish structure consisting of a stout central axis, bearing scales of two kinds: (*a*) small scales arranged spirally and developed directly on the axis; these are called the **bract-scales** (Fig. 325, B); (*b*) rather stouter scales developed one immediately above each bract-scale; these are called **ovuliferous scales**, because each bears two ovules on its upper surface (Fig. 325, A).

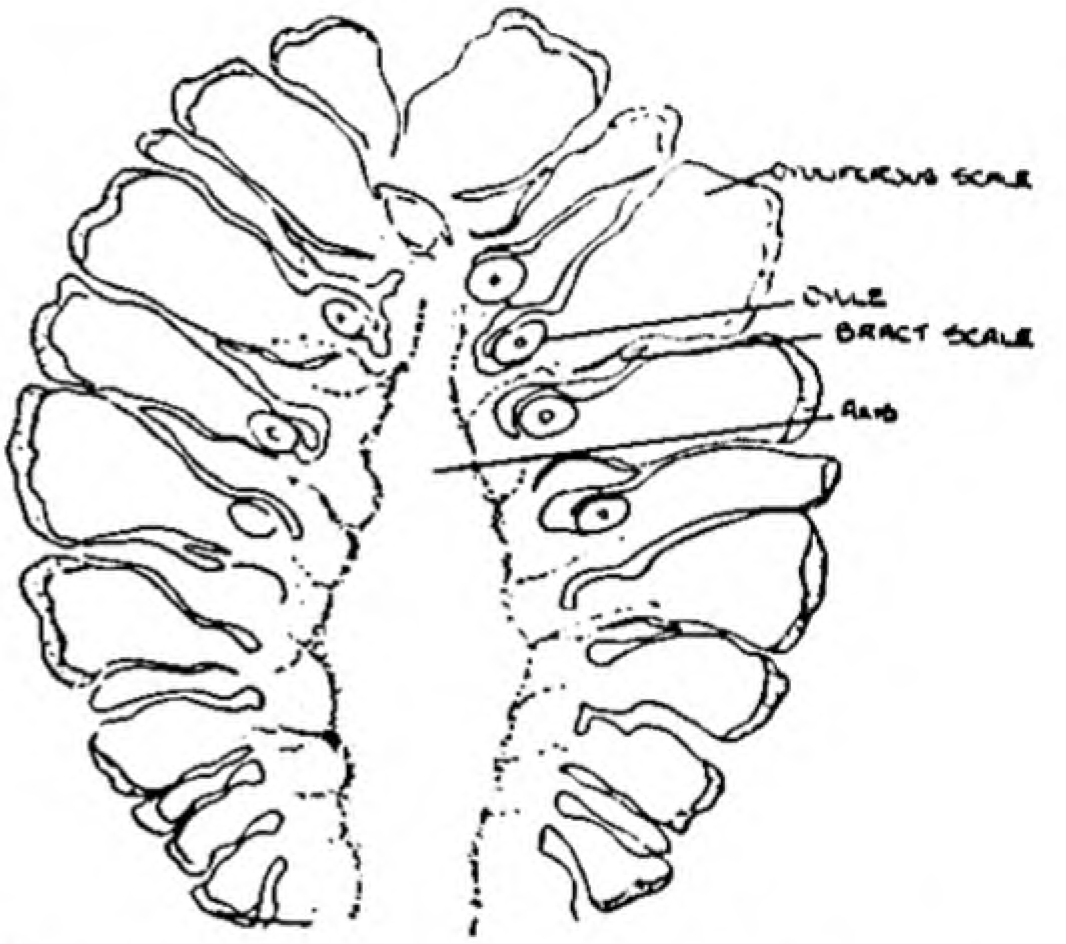

Fig. 324. LONGITUDINAL SECTION OF YOUNG FEMALE CONE OF *Pinus*.

The female cone of *Pinus* may be regarded either as a simple flower, or as an inflorescence. According to the former view the cone axis is a receptacle bearing open carpels, the bract-scales, each with a placental or ligular outgrowth, the ovuliferous scale. If viewed as an inflorescence, the cone axis is a rachis, and each bract-scale a true bract in whose axil is a modified shoot, the ovuliferous scale. The latter, bearing the ovules, would thus represent a flower. It is impossible at this stage to go into the arguments for and against these views. A far greater knowledge of the range of floral structure is necessary.

In *Pinus* the bract-scale remains small and is only visible in the very young, erect cone.

In some Gymnosperms, e.g. *Abies* (fir) and *Pseudotsuga* (Douglas-fir) the bract-scale grows as the cone develops and is still visible in the mature cone.

9. Structure of the Ovule (Fig. 326)

In the young female cone the ovule arises as a small cellular protuberance on the upper surface of the ovuliferous scale. This protuberance increases in size and becomes the nucellus. From its base arises a single integument which gradually invests the nucellus, except for a wide micropyle. The latter is directed obliquely towards the cone axis, and away from the junction of scale with axis.

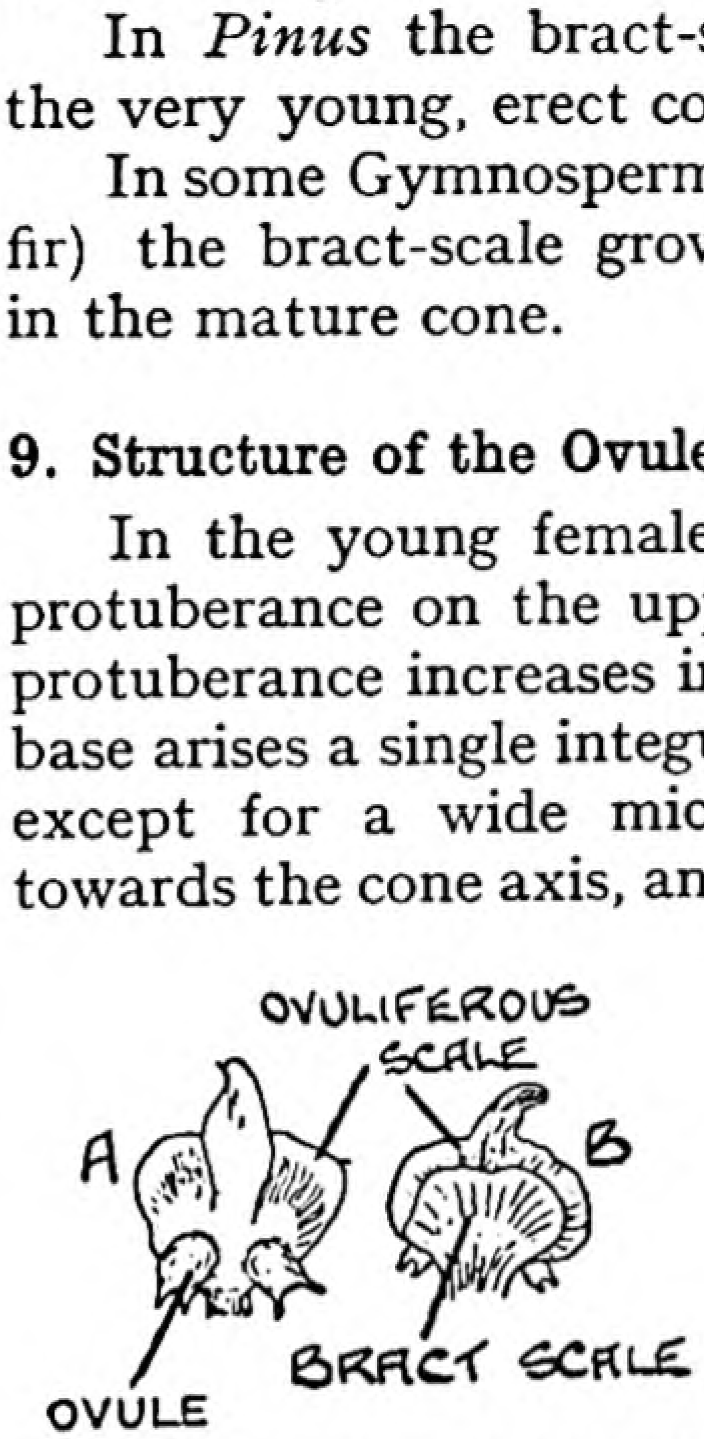

Fig. 325. Scales of Female Cone.

A, From above; B, From below.

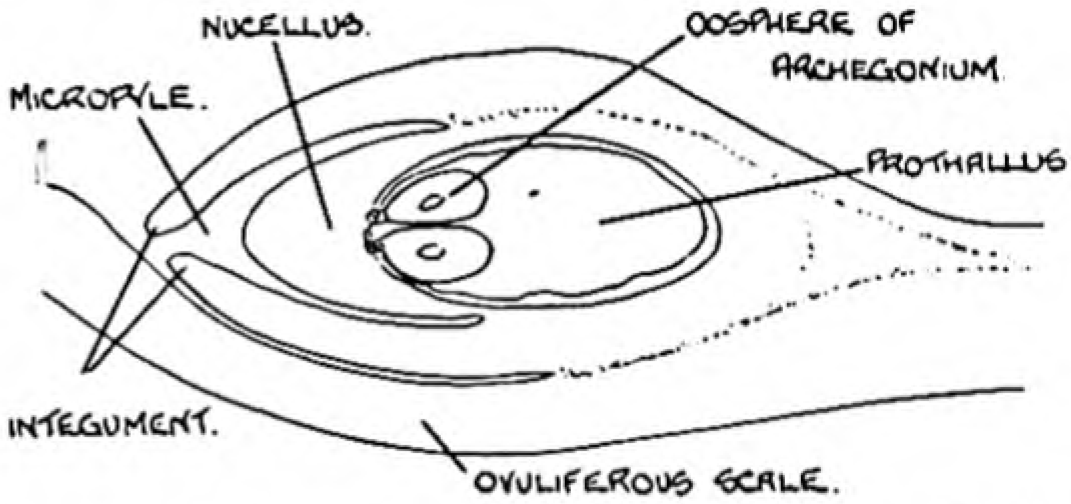

Fig. 326. Longitudinal Section of Young Ovule of *Pinus*.

At the apex of the nucellus, immediately below the epidermis, a hypodermal cell enlarges and becomes the archesporium. It divides, forming the tapetal cells and archesporial cell proper. The latter, now, embedded deeply in the nucellus, behaves as a spore-mother-cell and by meiotic division gives rise to four potential megaspores. Their nuclei have the haploid number of chromosomes. Only one of these megaspores matures and it is sometimes called the embryo-sac. At this stage the ovule is pollinated, but before tracing its development farther we must see how the pollen develops.

10. Development of the Microsporangium

Each microsporangium or pollen-sac is developed from a group of cells on the under surface of the male sporophyll. The wall of the sporangium is formed from the superficial layer and remains a single layer of cells. Several hypodermal cells, forming the archesporium, begin to divide rapidly. Tapetal cells are segmented from them towards the wall of the sporangium, and the remaining central portion forms a mass of microspore-mother-cells. Each of these mother-cells undergoes tetrad division, involving meiosis, to form four microspores or pollen-grains. The tapetal cells are disorganised during the development of the microspores.

11. Pollination

As in Angiosperms, the microspores have to be transferred to the neighbourhood of the megaspore. In *Pinus* this is effected by means of the wind, the transference being facilitated by the balloon-like expansions of the wall already described. *Pinus*, therefore, is *anemophilous*.

Pollination usually takes place about the end of May in N. Temperate regions. At this period the scales of the female cone open out, and separate from each other. The microsporangia split open, each along a median line and the microspores are liberated as clouds of yellow dust. Many are wasted, but some of the microspores are blown between the scales of the female cone and fall near the ovules. A mucilaginous secretion is given out from the micropyle. In this the microspores are entangled, and, as the mucilage dries up, they are drawn down the micropyle and finally come to rest on the apex of the nucellus. In the Gymnosperms pollination consists in the transference of the microspore, not to a stigma as in Angiosperms, but directly to the surface of the nucellus. The scales of the female cone close up after pollination and the cone bends back amongst the foliage leaves of the preceding year's growth.

12. Male Gametophyte

At first the microspore is unicellular. Even before it leaves the sporangium division begins, and it is completed on the surface of the nucellus. Two very minute rudimentary cells, the **prothallus-cells**, are cut off on one side. The remainder then segments into a small **antheridial cell** and a large **vegetative cell** (Fig. 327, A).

Comparing this with the germination of the microspore in *Selaginella*, there is an obvious suggestion that the small prothallus-cells represent a very rudimentary or reduced **male prothallus**. The antheridial cell is so called because, as will presently be explained, it produces the male gametes and is, therefore, the equivalent of the central cell of the antheridium of the Vascular Cryptogams, the male gamete being the homologue of the spermatozoid. The male gametes, however, are not motile. The large *undivided* vegetative cell probably corresponds to the peripheral cells which form the wall of the antheridium in *Selaginella*. In Gymnosperms there are definite cellulose walls formed between all these cells in the microspore.

In the further germination of the microspore on the apex of the nucellus, the large vegetative cell protrudes and elongates to form a slender pollen-tube (Fig. 327, B). The pollen-tube penetrates the tissue of the nucellus. Its destiny will be traced presently.

13. Growth of Female Cone—The Female Gametophyte

Continuing the growth of the ovule from § 9, although pollination is effected at this stage, fertilisation does not take place in *Pinus* till about a year later—some time in June of the second year. This, however, is not characteristic of Gymnosperms; in most of them fertilisation is effected in the same year as pollination.

In *Pinus*, during this protracted interval between pollination and fertilisation, many important changes go on in the ovule and in the cone as a whole. The cone increases in size and becomes green. During the winter these green cones are found at the apices of the shoots, just below the terminal winter bud. This increase in size is due to the enormous growth of the axis and of the ovuliferous scales. The bract-scales remain small, and are completely concealed. The growth is continued rapidly in the second year (Fig. 317). At the time of fertilisation the cones are large green structures, the rhomboidal areas on their outer surface being the outlines of the apices of the ovuliferous scales.

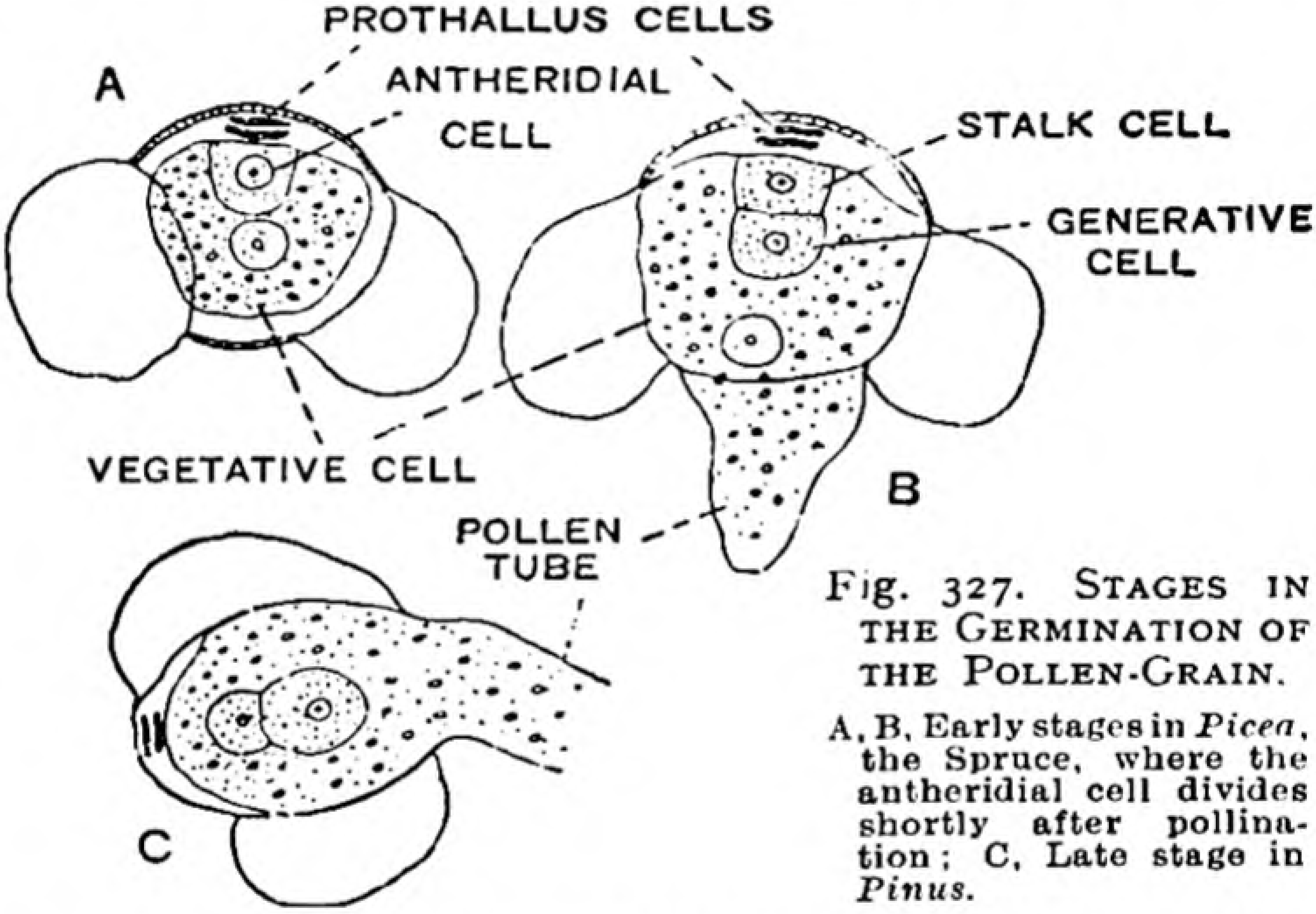

Fig. 327. Stages in the Germination of the Pollen-Grain.

A, B, Early stages in *Picea*, the Spruce, where the antheridial cell divides shortly after pollination; C, Late stage in *Pinus*.

Inside the ovule the megaspore becomes much larger, and there is formed *inside it* by cell division a mass of thin-walled parenchymatous tissue. If this process is compared with the germination of the megaspore in *Selaginella*, there will be no difficulty in recognising that the tissue formed in the megaspore is the **female prothallus** (Fig. 328).

Practically, the only important difference is that the megaspore in *Pinus* is not set free from the megasporangium, as it is in

Selaginella. But even in *Selaginella*, it will be remembered, the germination of the megaspore begins inside the sporangium.

The female prothallus in *Pinus* is enclosed in the nucellus. It has neither chlorophyll nor rhizoids. At its micropylar end are developed two or three **archegonia**. This completes the evidence of homology. The archegonium consists of a *venter* and a short *neck*. **Oosphere,** or female gamete, and *ventral canal-cell* are present, but there is no neck-canal-cell. The protoplasm of the oosphere presents a frothy appearance, owing to extensive vacuolation; it has no cell-wall. Except that no neck-canal-cell is formed, the development is essentially the same as in the fern or *Selaginella*.

14. Fertilisation

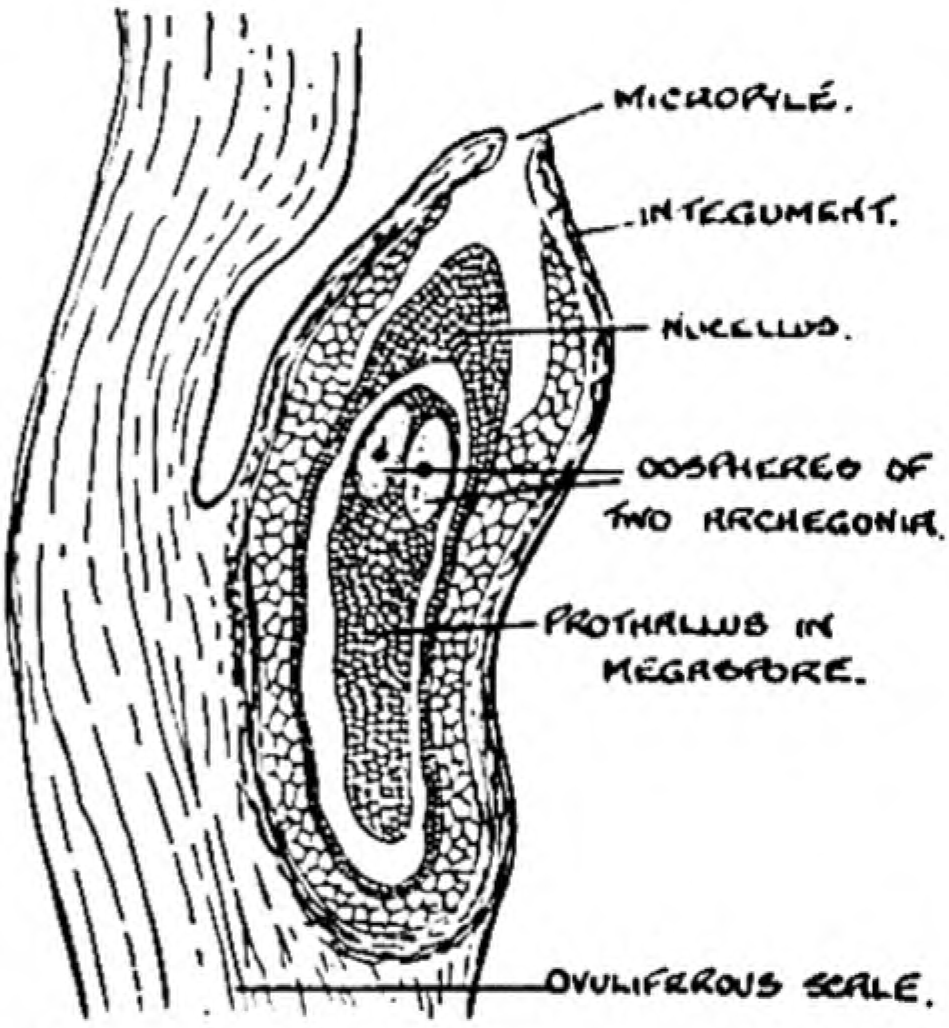

Fig. 328. *Pinus*. LONGITUDINAL SECTION OF MATURE OVULE.

In the first year the growth of the pollen-tube is arrested after it has penetrated a short distance into the nucellus. In the second year it again begins to grow. Some time in April the antheridial cell (§ 12) divides into two (Fig. 327, B), a barren cell called the **stalk-cell,** and a **generative cell.** The protoplasmic contents and nuclei of the large vegetative cell, the stalk-cell, and the generative cell, all pass down to the apex of the pollen-tube. Before this can take place, of course, the intervening cell-walls must disintegrate.

In the pollen-tube the naked generative cell divides into two cells, the *male gametes*. The pollen-tube ultimately reaches and enters an archegonium. One of the gametes only is concerned in the act of fertilisation. It passes from the pollen-tube into the oosphere, and its nucleus together with a small amount of cytoplasm fuses with the nucleus and cytoplasm of the oosphere. The fertilised oosphere forms a cell-wall and becomes the **oospore.**

15. Development of Embryo (Fig. 329)

The nucleus passes to the lower end of the oospore (*i.e.* the end away from the micropyle), and there, by repeated mitotic division, gives rise to four nuclei. These again divide, forming eight nuclei.

Cell-walls are laid down between the four basal nuclei, and in this way four small cells are formed at the lower end of the oospore. The rest of the oospore, with the other four (free) nuclei, which are afterwards disorganised, takes no share in the development; it contains food-material.

The four small cells divide into four rows of cells by two transverse walls; each row consists of three cells. These four rows elongate and push their way downwards into the tissue of the female prothallus, whose cells become stored with food-material to form the **endosperm** of the seed. The elongation is due to the formation of a long unicellular **suspensor** by the growth of the middle cell of each row. The four suspensors *separate from each other.* The cell borne at the end of each is **the embryonal cell**; it continues to divide and forms a potential embryo.

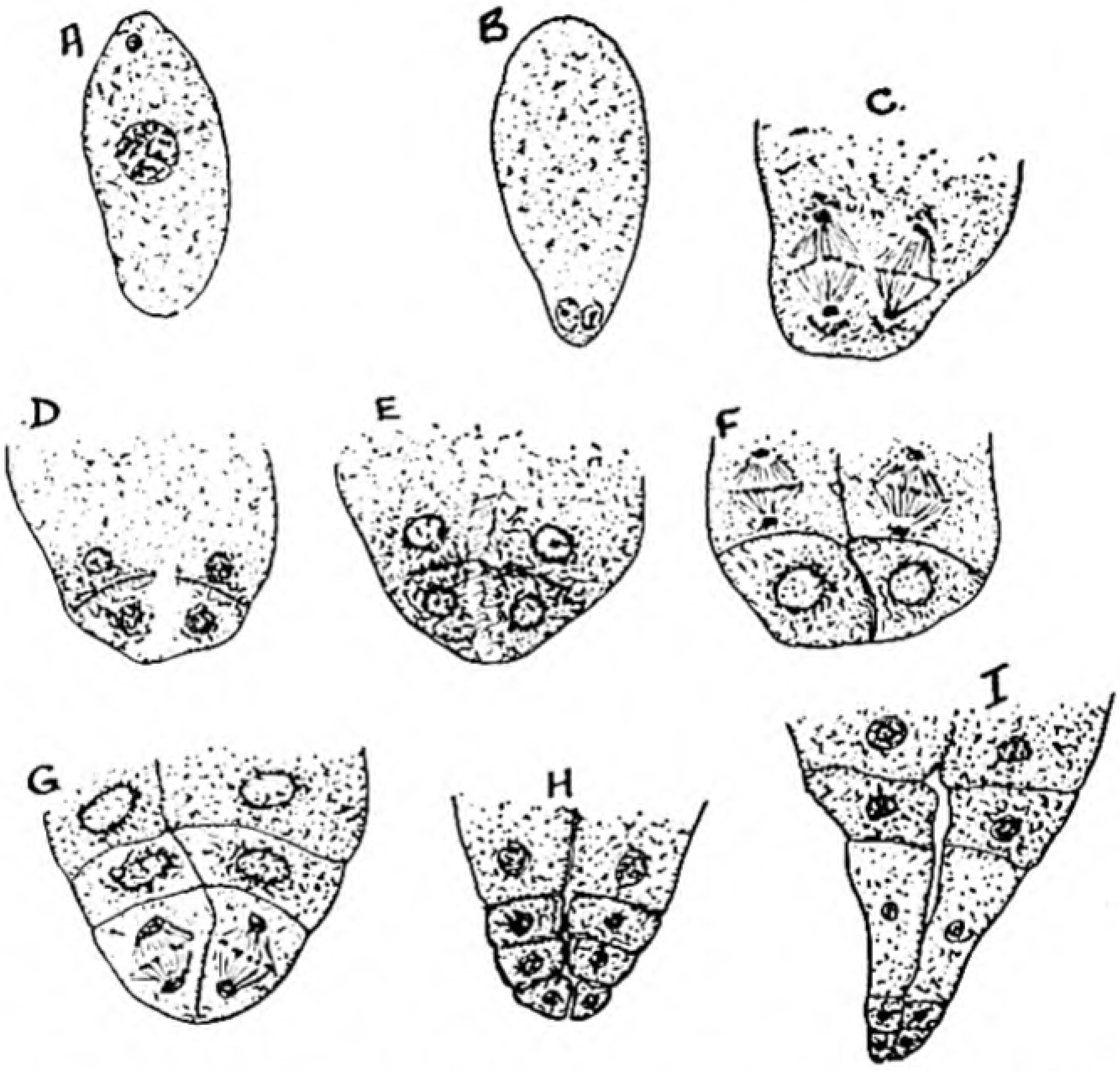

Fig. 329. *Pinus.* SEGMENTATION OF OOSPORE AND DEVELOPMENT OF EMBRYO.

Thus four potential embryos are formed from each oospore.* This is an example of *polyembryony* (see p. 271); it is characteristic of Coniferae. As more than one oosphere may be fertilised, many potential embryos may be present in one ovule. Only one, however, develops; the others die off. The suspensor takes no part in the development of the embryo.

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* In a few Coniferae, e.g. spruce, only one suspensor and one embryo are produced.

16. The Seed (Fig. 330)

The embryo which matures consists of a radicle, plumule and several cotyledons. It occupies a central position in the endosperm, which, as we have seen, is the tissue of the female prothallus stored with food-material supplied by the parent plant by way of the ovuliferous scale. The nucellar tissue is almost entirely disorganised, but a thin layer, containing some food-material, persists as a small amount of perisperm in the seed. The integument of the ovule becomes the *testa* of the seed. The upper surface of the ovuliferous scale separates as a thin membranous wing attached to the seed and assisting in its dissemination by wind. The female cone reaches maturity in the third year, and is then dry, brown and woody. Under dry atmospheric conditions the scales gape apart and allow the seeds to escape. Under humid conditions the scales fit closely together and protect the seeds. These movements of the scales are hygroscopic, and are induced by changes in atmospheric humidity.

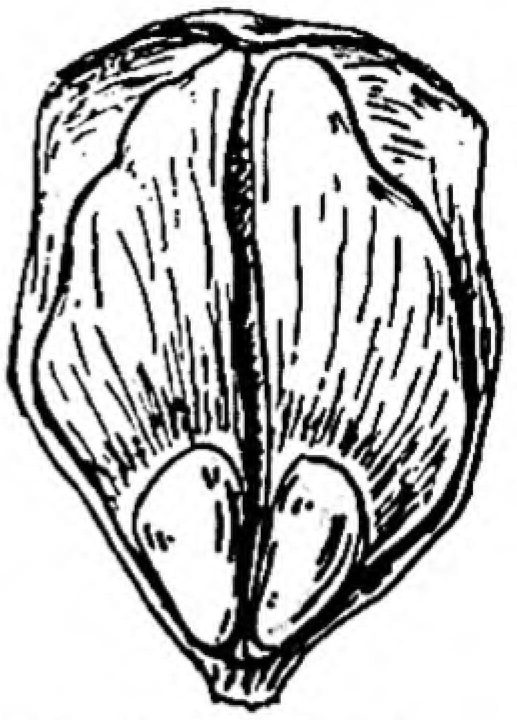

Fig. 330, A. Seeds on Scale, Surface View.

17. Germination

The cotyledons of *Pinus* may become green while still enclosed in the testa. They gradually absorb the endosperm and become epigeal, carrying the testa above ground. The radicle develops into a taproot. The first year's shoot, formed by the elongation of the plumule, has acicular green leaves arranged spirally and borne directly on the primary axis. As it continues to develop, however, the leaves become progressively smaller until they are mere scale-leaves, but they bear dwarf-shoots in their axils. Thus *Pinus* exhibits a "juvenile" form, which some regard as the primitive condition. This is more or less mesophytic and is sheltered by the ground vegetation. The later "adult" form is xerophytic. It is of interest to compare seedling development in *Pinus* with that in *Ulex* (gorse, pp. 138 and 214) and *Acacia* (p. 138) where we also have "juvenile" and "adult" forms.

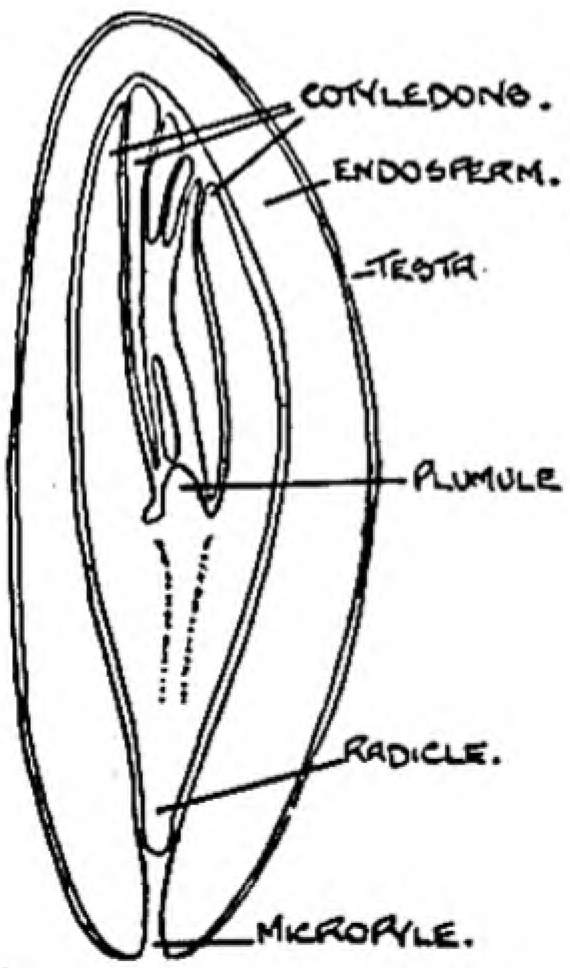

Fig. 330, B. Seed in Longitudinal Section.

18. Life History

The life history of *Pinus* may be graphically represented:—

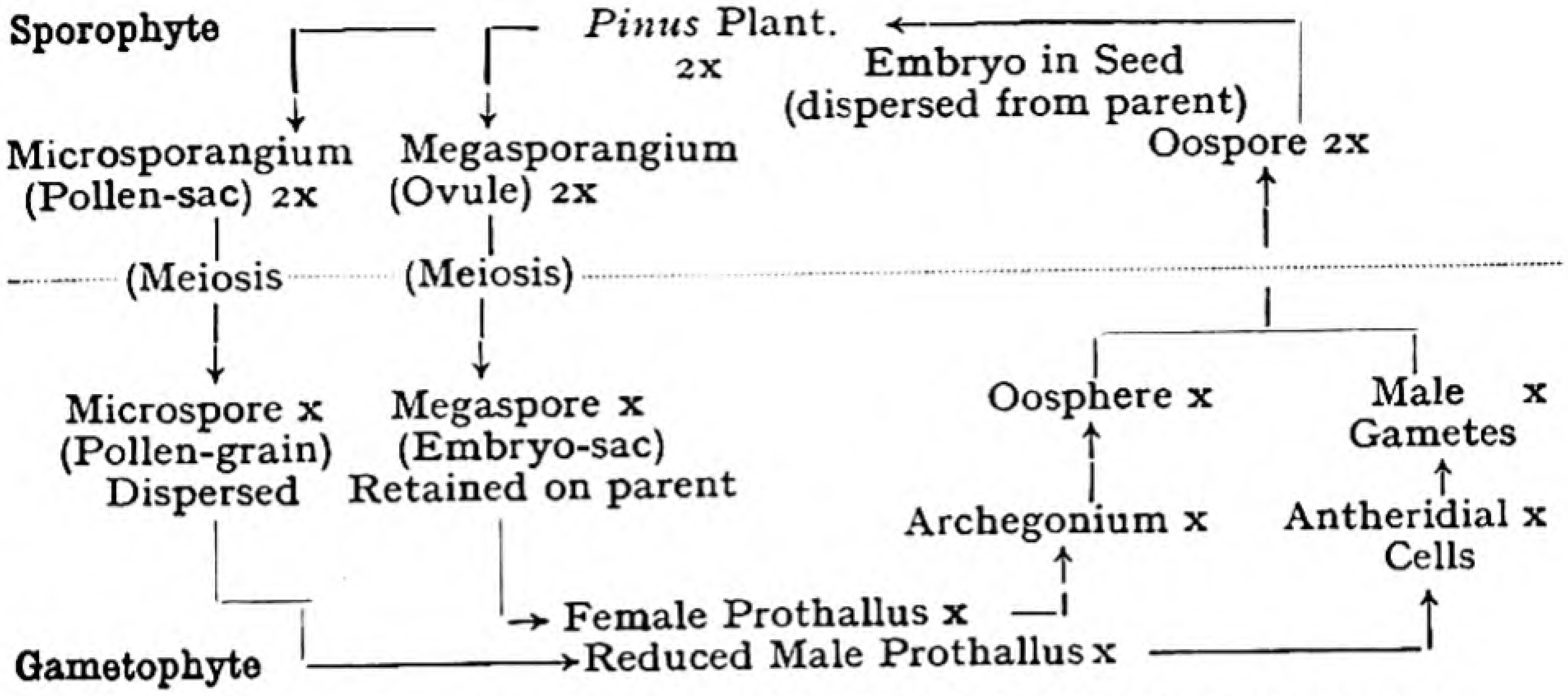
Sporophyte
Pinus Plant.
2x
Embryo in Seed
(dispersed from parent)
Microsporangium
(Pollen-sac) 2x
Megasporangium
(Ovule) 2x
Oospore 2x
(Meiosis
(Meiosis)
Microspore x
(Pollen-grain)
Dispersed
Megaspore x
(Embryo-sac)
Retained on parent
Oosphere x
Male x
Gametes
Archegonium x
Antheridial x
Cells
Female Prothallus x
Reduced Male Prothallus x
Gametophyte

Fig. 331. Life History of *Pinus* graphically represented. (x = the haploid number of chromosomes.)

B. Taxus baccata

19. General Characters

The yew is an evergreen tree with massive trunk and spreading branches, which may reach a height of 30 or 40 feet, found in the Himalaya. During its growth branching occurs from the base, and the branches fuse together to form the compound columnar trunk characteristic of the tree.

The linear, dark-green leaves (Fig. 333) have a short stalk-like portion which broadens into a flat base decurrent on the stem. The leaves are spirally arranged, but the shoots are dorsiventral owing to the positions which the leaves take up in relation to light.

The general internal structure resembles that of *Pinus*; but resin-ducts are absent.

20. The Flowers (Fig. 332)

The yew is dioecious. The male and female flowers are developed on different trees in the axils of leaves of the previous year. They are found on the under side of the branches, early in the year.

The *male flower* consists of an axis bearing 6-10 stalked peltate sporophylls. On the under side of the head of each sporophyll are 5-9 microsporangia. The microspores have no lateral expansions of the wall. At the base of the male flower are a number of scale-leaves which at first cover over and protect the young sporophylls.

The *female flower* arises as a bud, bearing a number of overlapping scale-leaves in the axil of a leaf of the previous year. The apex of this bud soon ceases to function, but in the axil of one of its upper scales there arises a short lateral shoot which bears a few scale-leaves and ends in a *single ovule*. The structure and development of the ovule are similar to those of *Pinus*.

21. Embryo and Seed

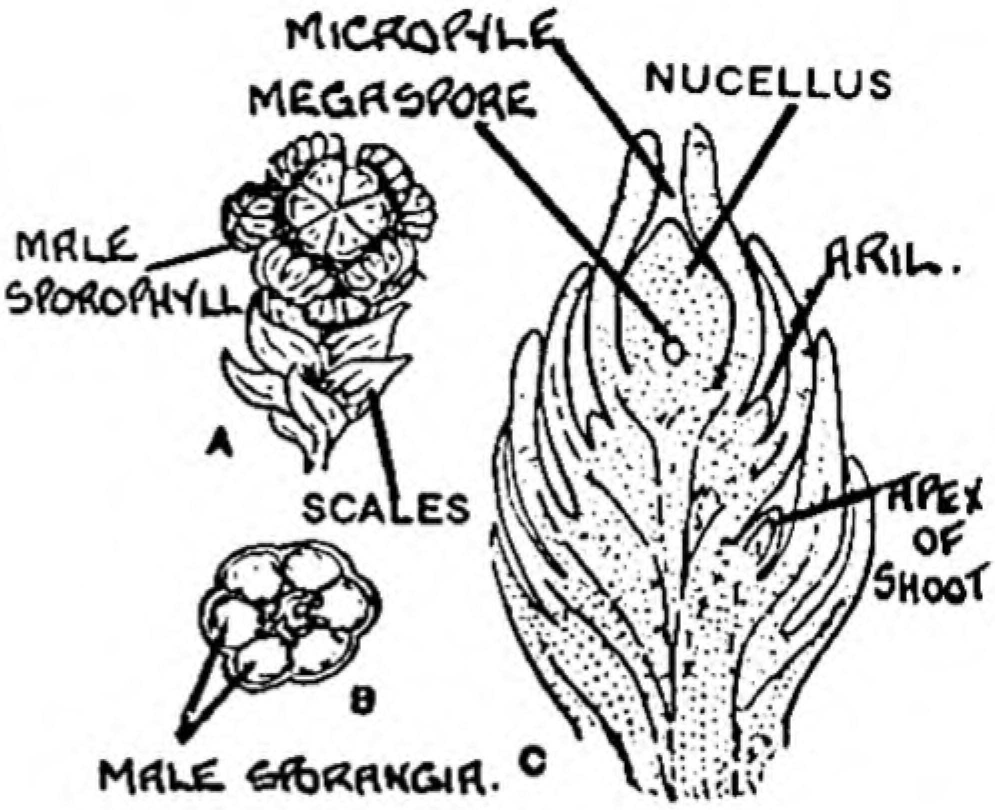

Fig. 332. FLOWERS OF YEW.
A, Male; B, Male sporophyll seen from below; C, Female, longitudinal section.

Pollination and fertilisation are effected as in *Pinus*, but in the same year. Only one embryo is developed from the oospore. During development, consequent on fertilisation, a cup-shaped structure grows up from the base of the ovule (Fig. 332). This is the aril. It becomes fleshy and forms the red investment of the ripe seed. The "fruit" or "berry" of yew is thus a seed with an investing aril (Fig. 333). The brightly coloured arils render the seeds attractive to birds which eat them with avidity. They do not appear to be poisonous to human beings, but the fresh green shoots have been known to poison cattle. It is not advisable, therefore, to have yew growing where it is accessible to cattle.

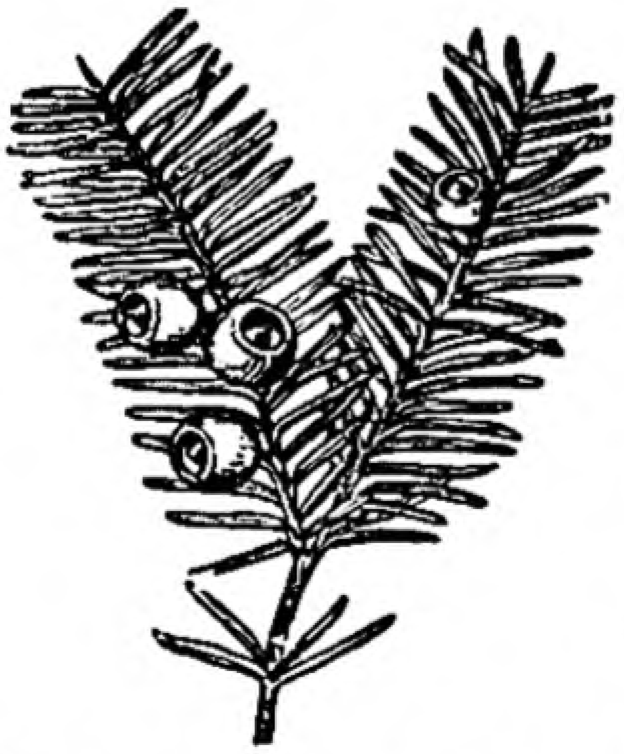

Fig. 333. TWIG OF YEW WITH "FRUITS."

C. JUNIPERUS

22. General Characters

The junipers generally form small, profusely-branched trees or bushes, although *Juniperus recurva* may reach a height of from thirty to forty feet in the Himalaya, where many species of *Juniperus* occur. The leaves, which are always born directly on the main stem and not on dwarf shoots, are usually small and appressed to the stem, but needle-shaped leaves occur in, e.g., *J. communis* and *J. oxycedrus*. Male cones are produced in leaf axils. Each cone has a central axis with small scale-leaves at the base and several whorls of peltate sporophylls. Two to four microsporangia develop on the lower side of the microsporophyll. Like the male cones, the female cones occur in leaf axils and have scale-leaves at the base succeeded by a whorl of megasporophylls, each with a single upright ovule in the alternating position.

The microsporangia shed their microspores (pollen) but pollination and fertilisation are often separated by a considerable period of time (e.g. about 12 months in *J. communis*; cf. *Pinus*, p. 414). After fertilisation the bases of the megasporophylls become succulent and cohere above the seeds, although the line of demarcation between the sporophylls remains evident at the apex. The succulence of the megasporophylls and their subsequent fusion gives the whole structure the superficial appearance of a berry.

D. CYCAS

23. General Characters

Representatives of the Cycadales existed during the Mesozoic period, when they attained their greatest development. The fossils are represented chiefly by leaves, and a few stems and reproductive organs. Of living Cycadales, four genera belong to the New World and five to the Old. Of these latter *Cycas* has about 20 species, extending through tropical Asia, and across the eastern islands to Australia. *Cycas revoluta* is the "sago-palm" of China and Japan.

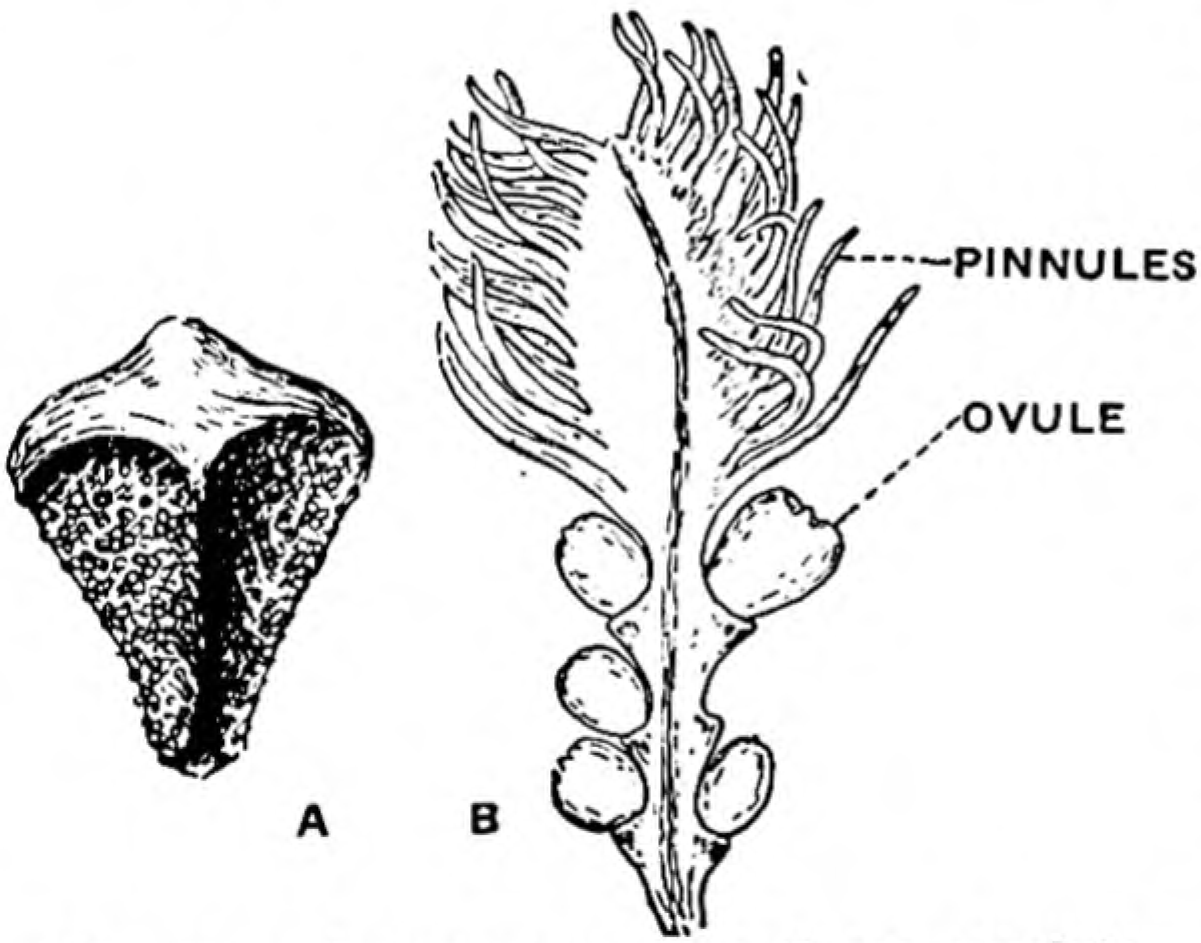

Fig. 334. SPOROPHYLLS OF *Cycas revoluta*. A, Male; B, Female.

The stem of *Cycas* is usually unbranched, short and stout, the older part covered with leaf-scars, or leaf-bases, the top bearing a crown of spirally arranged leaves of two kinds, brown scale-leaves alternating with large simply pinnate foliage leaves. The pinnae are hard in texture and of xerophytic structure, with thick cuticle and sunken stomata. The whole appearance is reminiscent of a tree-fern.

A tap-root system is developed and the lateral roots may send up vertical aerial rootlets with branches so close together that they form coral-like masses. These roots may develop cortical spaces which become inhabited by colonies of *Nostoc* (Cyanophyceae).

The stem of *Cycas* has a large pith, a relatively narrow vascular cylinder of collateral endarch bundles and a thick cortex traversed by leaf-trace bundles which frequently run in a tangential direction and form numerous "girdles." Mucilage canals occur in both cortex and pith. The tracheides of the xylem have numerous "multiseriate" pits.

The bundles entering a petiole assume a regular "omega" arrangement (℧), and each bundle is mesarch, but the metaxylem is developed mainly in the centripetal direction from the protoxylem, although there is a small quantity of centrifugal metaxylem. The protoxylem thus occupies the centre of the bundle and the phloem lies outside it. (In *Stangeria* the traces in the leaf-base are actually concentric, and *Cycas* has a cortical system of concentric bundles.)

Secondary thickening in the stem involves the formation of a cambium which develops secondary xylem to the inside and secondary phloem to the outside. This cambium then ceases its activity and a new cambium arises outside the secondary zone formed by the first cambium and behaves like it. A third cambium may arise outside the second zone, and so on, and so concentric rings of xylem, phloem and parenchyma may occur, repeated twice or thrice in older stems.

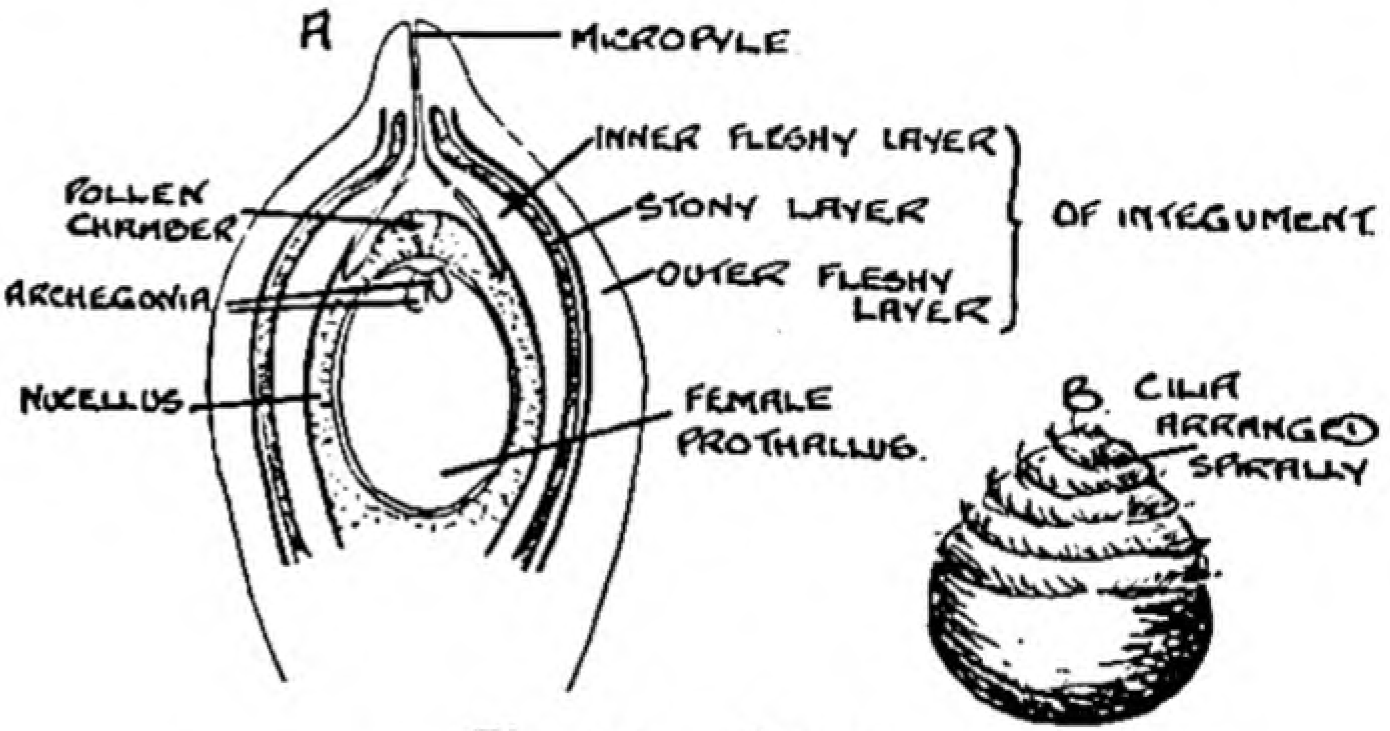

Fig. 335. *Cycas*.
A, Longitudinal section, Ovule; B. Spermatozoid.

24. Reproduction

Cycas is dioecious. The microsporangiate cone is terminal to the stem apex. The growth of the stem is continued by a lateral bud and is therefore sympodial. The flat microsporophylls are arranged in a compact spiral on the axis. The apical and basal scales are sterile whilst the remainder bear microsporangia collected in clusters or sori of 3-5 on their lower (abaxial) surfaces (Fig. 334, A).

The megasporophylls of *Cycas* are not arranged in a true cone but occupy a position in between foliage and scale-leaves in the development of the main axis, which is therefore monopodial. The sporophylls are pinnate, like the foliage leaves, but much reduced, and the ovules are borne on the lower margins of each sporophyll, occupying the positions of the two rows of lower pinnae. The number of ovules varies from two to ten per sporophyll (Fig. 334, B).

The megasporophylls of the other genera of the Cycadales (e.g. *Macrozamia*, *Encephalartos*, etc.) are aggregated into cones which may be of great size, and the sporophylls have not the leaf-like character of those of *Cycas*. Each is generally a shortly-stalked structure bearing two ovules (megasporangia).

25. Structure of the Ovule (Fig. 335, A)

The ovule is surrounded by a thick integument which becomes three-layered, fleshy on the outside and inside, stony between. The micropyle leads to a cavity in the beaked apex of the nucellus, known as the pollen-chamber, and the floor of this chamber, which separates it from the cavity of the megaspore, becomes soft and ultimately disintegrates to form a cavity. By the division of the nucleus of the megaspore, free cell formation gives rise to a female prothallus. At its apex, just below the floor of the pollen-chamber, three to six archegonia arise. Each consists of a short neck, a ventral canal-cell and an oosphere. The necks open into a depression which forms in the apex of the prothallus just below the floor of the pollen-chamber, and which fills with fluid, and the disorganisation of the floor of the pollen-chamber already mentioned brings about access from the pollen-chamber to the necks of the archegonia.

Meanwhile microspores, disseminated by the wind, are caught in the mucilaginous exudation from the micropyle of the ovule. As this dries the meniscus recedes and draws the microspores into the pollen-chamber. Each microspore germinates much as in *Pinus*, but the pollen tube grows into the nucellar wall of the pollen-chamber and becomes an absorptive organ. Inside the microspore a reduced male prothallus gives rise to two male gametes each of which becomes somewhat top-shaped and, along a spiral line running from the pointed end towards the broader end, numerous cilia arise (Fig. 335, B). These male gametes are therefore ciliated, motile, spermatozoids and, when liberated into the pollen-chamber, one swims to an archegonium, enters it and fuses with the oosphere to form an oospore.

26. Seed Structure and Germination

Repeated division of the oospore nucleus produces a large number of free nuclei. Ultimately, however, a cellular embryo is produced, with two cotyledons, and a radicle embedded in a coleorhiza. A suspensor pushes the embryo into the tissue of the female prothallus. The three-layered integument becomes the seed-coat, but the inner layer shrivels. On germination the coleorhiza protrudes; the radicle emerges from it and becomes the tap-root. The hypogeal cotyledons absorb food from the remains of the female prothallus. The growing plumule shows transition from scale-leaves to pinnate foliage leaves.

CHAPTER XVI

COMPARISON OF THE PTERIDOPHYTA AND SPERMATOPHYTA

1. Pteridophyta

The earliest known Pteridophyta are represented by fossil remains in the Silurian and Early Devonian rocks. The plant-body in some was Alga-like in external appearance, but internally there were true vascular bundles. These plants may have evolved from an algal ancestor, but there are no known intermediate forms, and any assumed relationship between them must be based on a hypothetical common ancestor still earlier in geological history. These primitive Pteridophyta were homosporous. Other homosporous forms of about the same age showed an external resemblance to our present-day Lycopods.

We have seen that amongst the heterosporous forms it is possible to arrange existing types in such a way as to suggest a graduation from homospory to heterospory. Thus, for example, we have the series *Lycopodium*, *Equisetum*, and *Selaginella*. There is, however, no evidence that heterosporous forms evolved from homosporous ones. It must be borne in mind that fossil evidence is necessarily incomplete since relatively few plants of these very early floras have been preserved as fossils, and the specimens that have been preserved are largely fragmentary.

Available evidence points to an independent appearance of heterospory in different groups of plants. One of these groups, Lepidodendraceae, existed from Devonian, through Carboniferous into Permian times. They were tree-like, and their stems showed secondary increase in thickness. Our coal-measures abound with their remains, along with those of plants related to present-day horse-tails and ferns. Frequently they are so well preserved in siliceous masses known as coal-balls, that rock-sections can be cut and examined under the microscope, and the detailed anatomy of roots, stems, leaves and reproductive organs studied. Woody tissues are particularly well preserved.

The living heterosporous Pteridophyta are marked by possessing microsporangia and megasporangia. The former bear numerous microspores, the latter usually four megaspores. Both microspores and megaspores are shed from their sporangia. A problem which now confronts us is the relating of this condition with that prevailing in the Spermatophyta where the megasporangium bears only one megaspore which it retains.

Tertiary (Recent)	Pleistocene	
	Pliocene	
	Miocene	
	Oligocene	
	Eocene	
Secondary (Mesozoic)	Cretaceous	Chalk, etc.
		Wealden, etc.
	Jurassic	
	Triassic	
Primary (Palaeozoic)	Permian	
	Carboniferous	Coal Measures, etc.
		Carboniferous Limestone
	Devonian and Old Red Sandstone	
	Silurian	

Fig. 336. Showing Sequence of Rocks of Earth's Crust to Illustrate Relative Positions of Fossil-bearing Strata.

Clues to the possible origin of the seed habit are found amongst fossil Pteridophyta of the later horizons. In certain Lepidodendraceae only one of presumably four megaspores persisted in the megasporangium, and the latter was almost completely enclosed within an outgrowth from the sporophyll. But there is a big difference between this condition and that found in the earliest known plants bearing true seeds, the Pteridosperms, which existed from Lower Carboniferous to Jurassic times. The gap cannot at present be filled.

The Pteridosperms resembled our modern tree-ferns in habit, but their stems and roots show secondary thickening. Their leaves were like fern-fronds. Some of these bore microsporangia of a type comparable with the sporangia seen in existing ferns; they were numerous and on the lower surface of the segments of the frond which was thus a microsporophyll. Megasporangia terminated the segments of, apparently, other fronds. Evidently only one megaspore persisted in the megasporangium, and its wall was attached to the inner wall of the sporangium. An integument enclosed the sporangium except for an opening at the apex (the micropyle), and a cup-like structure (the cupule) was present outside the integument. Such a structure is an ovule, and whilst it cannot be related (except hypothetically) with anything that has preceded it, it does, on the other hand, closely resemble the ovule of the Cycadales (see *Cycas*, p. 420). In fact, the comparison is so close that it is difficult to avoid the assumption that " pollination " and fertilisation occurred in both groups in the same way.

Although the Pteridosperms show affinities with the ferns, they are an independent group, and probably quite as old. There is no evidence that they were derived from the ferns, but both groups may have had a common ancestry and then developed along parallel lines. The Pteridosperms are usually regarded as the most highly organised group of Pteridophyta, though they might be classified as Gymnosperms. The latter do not derive from them, however, although, as we have seen, the Cycadales, and also other primitive Gymnosperms, show certain probable connexions.

2. Spermatophyta

Amongst living Gymnosperms the Cycads, throughout their known history, have retained to a remarkable degree what are regarded as primitive characters. They, along with *Ginkgo* (the maiden-hair tree), possess motile spermatozoids, and in this and certain other features show affinities with the Pteridophyta. They are not, however, in the same line of descent as the more advanced Coniferales, since fossil representatives of the latter can be traced to strata at least as old as those bearing Cycadales. True gymnospermous wood fossilised in Mid-Devonian rocks has a structure as highly organised as the secondary wood of living Conifers. From this time on, through Triassic and Jurassic periods, group after group appear, reach their maximum development, and disappear. Forms obtained from the Jurassic beds are clearly relatable to such living types as *Araucaria* (the monkey-puzzle). They become more numerous in the Cretaceous, and in Tertiary times many existing species had already appeared.

3. Gymnosperms and Angiosperms

An important character common to Gymnosperms and Angiosperms is the production of seeds. A seed is developed from an ovule as the result of fertilisation. An ovule may be defined as an integumented megasporangium.

Each megasporangium consists of a nucellus invested by one (Gymnosperms) or two (most Angiosperms) integuments, except for a narrow pore, the micropyle, leading to the tip of the nucellus. One megaspore (the embryo-sac) is embedded in the tissue of the nucellus.

The manner in which the ovule is borne varies. In some Gymnosperms it terminates an axis (e.g. *Taxus*), in others it is borne on the margin of a leaf-like sporophyll (e.g. *Cycas*), again in others it is borne on the surface of a scale not so obviously leaf-like. It is characteristic of the Gymnosperms that the ovules are " naked," whereas in Angiosperms they are borne inside a closed structure, the ovary.

The microspores (pollen-grains) are borne in large numbers in microsporangia (pollen-sacs) associated with microsporophylls (stamens).

The interpretation of the true morphological nature of stamens and carpels is based on comparative morphology and has an important bearing on the theory of the structure of the flower in Angiosperms.

The microspores are carried to the ovules (Gymnosperms), or to the stigmas of the ovaries (Angiosperms), by the agency of air-currents, insects, birds, or, rarely, water-currents. Here they germinate to produce a reduced gametophyte resulting in two male gametes which, in Cycadales and Ginkgoales are motile spermatozoids, but in all other forms are non-motile nuclear bodies.

The megaspore " germinates " within the nucellus of the ovule. In the Gymnosperms it becomes filled with a cellular prothallus bearing one or more recognisable archegonia at the end nearest the micropyle. In the Angiosperms the mature megaspore (embryo-sac) contains no recognisable archegonium or prothallus but a few " cells," one of which is the oosphere.

An oosphere, on being fertilised by a male gamete, becomes an oospore and develops into an embryo. In the Gymnosperms the prothallus simultaneously becomes a repository for nutritive material and is now called endosperm. In Angiosperms, the endosperm develops as a post-fertilisation product, and in non-endospermous seeds food reserves are stored in the embryo. The integument(s) give rise to the testa, a protective covering, and the micropyle persists. Thus the ovule develops into a seed. In the Gymnosperms, since there is no ovary, there is no fruit, but exceptionally, fruit-like bodies may occur (e.g. juniper " berries ") as the result of changes taking place in the protecting scale-leaves after fertilisation.

The seeds (or fruits) are dispersed from the parent plant by various agencies, and, after a period of rest, germinate. The embryo draws upon the stored food-material provided by the parent sporophyte until it becomes established as an independent plant. The gametophyte is never independent.

The investigations of cytologists into nuclear behaviour during all these changes have served to bring out the precise limits of the two generations and to emphasise the homologies of the Spermatophyta with the Pteridophyta. The microspores within the microsporangium and the single megaspore within the nucellus of the ovule, are the result of a tetrad division, involving meiosis, of a spore-mother-cell. The haploid number of chromosomes characterises the cell-divisions of both micro- and mega-spore during germination, up to the production of male and female gametes. The fusion of a male with a female gamete results in an oospore which thus has a diploid nucleus and is the beginning of the sporophyte generation.

It will be helpful at this stage to compare the life histories of the members of the Pteridophyta and Spermatophyta as set out diagrammatically in Figs. 302, 304, 314, 331 and 337. In order to render comparison easier, the facts have been arranged in the same sequence. It is important to notice the exact delimitation of gametophyte and sporophyte generations, and the progressive reduction of the gametophyte from an independent, self-supporting plant to a minimum of essential gametes and one or few accompanying cells. On the other hand, the sporophyte may assume considerable proportions and be highly differentiated. Externally this differentiation is seen in the division of labour between vegetative and reproductive parts of the shoot, and ultimately in the extreme specialisation of the flower as seen in the Angiosperms.

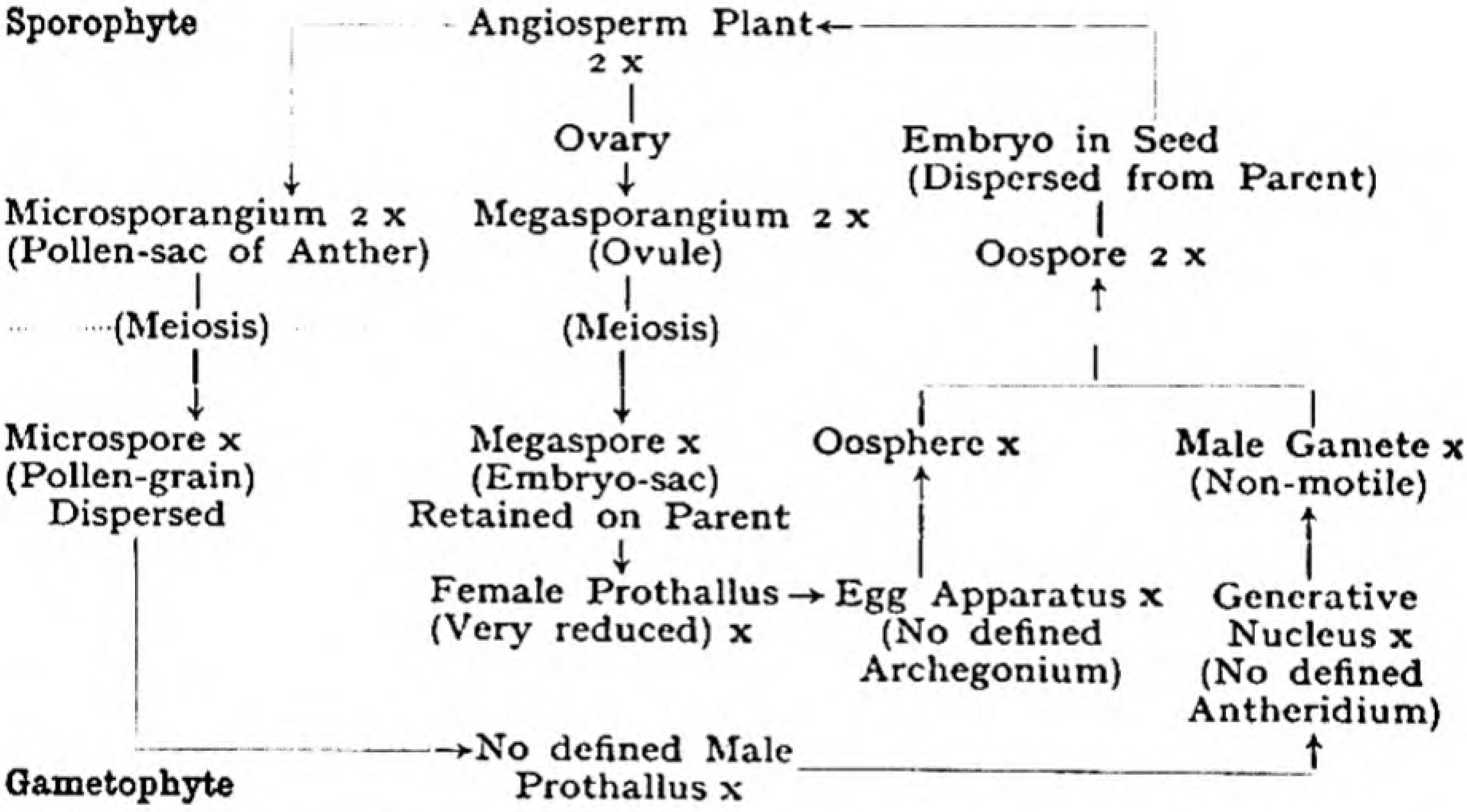
Sporophyte
Angiosperm Plant 2 x
Ovary
Embryo in Seed (Dispersed from Parent)
Microsporangium 2 x (Pollen-sac of Anther)
Megasporangium 2 x (Ovule)
Oospore 2 x
(Meiosis)
(Meiosis)
Microspore x (Pollen-grain) Dispersed
Megaspore x (Embryo-sac) Retained on Parent
Oosphere x
Male Gamete x (Non-motile)
Female Prothallus (Very reduced) x
Egg Apparatus x (No defined Archegonium)
Generative Nucleus x (No defined Antheridium)
No defined Male Prothallus x
Gametophyte

Fig. 337. LIFE HISTORY OF ANGIOSPERM GRAPHICALLY REPRESENTED. (x = the haploid number of chromosomes.)

CHAPTER XVII

THE ORIGIN OF THE FLOWER AND OF THE FLORAL ORGANS

1. Living Angiosperms are so highly organised that it is quite impossible, from their study alone, to form any decisive conclusion as to the homologies of the flower and its parts. Systematists do not altogether agree on the question of which is the simplest (most primitive) type of flower. Forms may have reached apparent simplicity by reduction from more complex organisation.

2. The Primitive Flower

It is only necessary here to mention two prevailing views on the most primitive type of floral construction in the Angiosperms:

(*a*) That represented by the Fagales and allied plants. The flowers are unisexual, arranged in catkins or compound inflorescences. and the plants are monoecious.

(*b*) That represented by such orders as the Magnoliales (e.g. tulip-tree and magnolia) and Ranales. The flower is hermaphrodite, the parts have a spiral arrangement on a conical or club-shaped axis (receptacle) and are free.

For the elucidation of this problem evidence is adduced from comparative morphology of living and fossil plants.

3. Floral Morphology

The generally accepted view of floral morphology has been that the flower is homologous to an axis (receptacle) bearing sporophylls, the lower ones of which have been modified (including sterilisation) to form a perianth.

The nearest approach to such a structure outside the Angiosperms is the cone or strobilus of the Gymnosperms. In all the types we have described the cones are unisexual or monosporangiate, and are of two kinds, the male or staminate cone bearing microsporangia, the female or ovulate cone bearing megasporangia. The existence of monosporangiate cones in the Gymnosperms might be regarded as providing evidence in favour of the Fagales-type of Angiosperm being primitive.

The earliest seed plants, the Pteridosperms, did not possess cones. They showed a distinction between vegetative leaves and sporophylls, but did not have the latter aggregated into a specialised fertile shoot. But there is a group of fossil Gymnosperms, the Cordaitales, contemporaneous with the Pteridosperms, which had strobili, and these were monosporangiate. The microsporangiate strobilus had a stout axis bearing a number of spirally-arranged bracts, among which were the microsporangia (stamens). The latter were either single, or grouped, near the tip of the axis. Each stamen consisted of a stalk, terminating in a cluster of three to six sporangia. The megasporangiate strobili were similar, except that in the axils of some of the bracts there was a dwarf shoot bearing small bracts and terminating in an ovule. The ovule had two integuments, as in Angiosperms, but the nucellus was free from the integument. The seeds are scarcely distinguishable from those of the Pteridosperms. Thus even the earliest known Gymnosperms had monosporangiate strobili or cones.

On the other hand, in the Jurassic period, we have remains of Gymnosperms with bisporangiate strobili, that is, both microsporangia and megasporangia borne in the same strobilus. Of particular interest is *Cycadeoidea* (*Bennettites*). This plant bore an external resemblance to the Cycads, but possessed reproductive shoots of limited growth. These were so much like flowers that the same terminology has been used in their description. The strobili were numerous and borne laterally. Each strobilus had numerous "perianth leaves" surrounding a whorl of 18 to 20 "stamens" on a convex "receptacle" terminated by a "gynaeceum." The stamens were pinnate microsporophylls, like fern fronds, about 10 cm. long, each pinna bearing two rows of microsporangia comparable with fern sporangia. The gynaeceum was formed of numerous peltate scales protecting, between them, ovules terminal to long stalks. Older "flowers" have seeds containing embryos with two cotyledons but no endosperm, and a testa formed of the single integument.

There is no evidence as to how this bisporangiate type of strobilus seen in *Cycadeoidea* arose, but there is a suggestion of its persistence in a group of living Gymnosperms, the Gnetales, and of the possible derivation of the monosporangiate condition from it.

The Gnetales are interesting in that, among other things, they show Angiospermous tendencies in possessing true vessels in their secondary xylem. There are three genera, *Gnetum*, *Ephedra* and *Welwitschia*. The ovulate strobilus of *Ephedra* consists of a short axis bearing numerous pairs of scale-like bracts. Terminating the axis of each strobilus we have one, two or three ovules, each with one integument, and below it a structure which appears to be formed of two fused scale-leaves. There is some basis for comparing this "gynaeceum" with that of the Cordaitales, and also of *Cycadeoidea* (bereft of its stamens). Another point of interest is that male strobili of *Ephedra* have been found possessing aborted ovules, and so partake of the bisporangiate character. We might infer from this that the monosporangiate condition is derived from the bisporangiate. This is further exemplified in *Welwitschia,* where male " flowers " consist of a whorl of six simple stamens surrounding a rudimentary ovule. We can imagine such a structure to be derived from *Cycadeoidea* by assuming a reduction in the whorl of stamens to six, and in the collection of ovules to one. In *Gnetum* the strobilus consists of an axis bearing a cup-like structure, which appears to be formed of two fused scale-leaves, surrounding a series of " stamens " which in turn surround a cluster of " ovules." One of the latter terminates the strobilus. The ovules have two integuments. Comparing this with an angiospermous flower, the cup-like structure might be equivalent to the perianth, and the stamens and ovules to the androecium and gynaeceum respectively. This type of structure would link the bisporangiate strobilus of *Cycadeoidea* on the one hand, and the hermaphrodite flower of Magnoliales on the other. But the problem is not so simple as it appears on the surface. The question of the morphology of the " stamens " and " ovules " of these types has to be faced, and this, too, bristles with difficulties.

4. The Stamen

The angiospermous stamen has been generally regarded as homologous with a microsporophyll. The Pteridosperms and Bennettitales have microsporophylls comparable with fern fronds, and the Cycads have microsporangia grouped into " sori " on the under surface of an expansion which, however, is not leaf-like in appearance. Amongst the Coniferales, male cones may be composed of structures resembling scale-leaves, bearing microsporangia on their lower surfaces. These, and other examples appear to point to the foliar origin of the stamen.

But in the Cordaitales we noticed that the " stamens " were borne amongst bracts, and that each consisted of a stalk terminating in one or more microsporangia, that is, they were not foliar, but more probably stem structures. Also some of the earliest known Pteridophyta had a Lycopod-like habit, but their sporangia were not borne on leaves. Again, in the Gnetales, individual " stamens " have a " perianth " on the stalk below the sporangia, and are subtended by a " bract." If this interpretation is correct each " stamen " is a flower, much as the similar structure in *Euphorbia* (spurge), and therefore not foliar but stem-like. Recent work along entirely new lines suggests that angiospermous stamens originate at the growing point in the way common to stems and not leaves, and so is against the view of their foliar nature.

It is clear, therefore, that the homology of the stamen must remain an open question until more definite evidence is forthcoming.

5. The Carpel

The classical interpretation of the carpel as a leaf bearing marginal ovules (megasporangia) and folded in such a way as to enclose the ovules in an ovary, is also open to doubt. Indeed, there appears to be less support for the foliar nature of the carpel than for that of the stamen. It is tempting to compare a carpel such as gives rise to a follicle or legume, split along its ventral suture, and opened out, with the megasporophyll of *Cycas*. Thence it is possible to imagine a step backwards to the apparently foliar megasporophylls of the Pteridosperms.

But against this, we have the evidence of the Cordaitales, Bennettitales, Ginkgoales, many Coniferales and Gnetales, in none of which is the ovule borne on a leaf, or, indeed on a structure which need be interpreted as a leaf. Even in considering the female cone of *Pinus* we suggested the possibility of regarding the ovuliferous scale as axillary to the bract-scale, in which case it would be a stem structure, and the cone an inflorescence.

6. Summary

It will be seen that the available evidence is insufficient as yet to solve the problems of the origin of the Angiosperms, the morphology of their flowers or the homologies of their floral organs. Interpretations which at first appeared to be straightforward and natural have been called into question as our knowledge has increased. The attempt to solve these problems has stimulated research, and has provided material on which various hypotheses have been based. It is important, however, to separate facts from hypotheses which are elaborated from them. Facts are incontrovertible; hypotheses may have to be abandoned as fresh facts come to light. In forming an hypothesis an attempt is made to fit apparently disconnected facts into a definite pattern; assumptions are made which may prove to be false in the light of later discoveries. But the pursuit of knowledge is, in itself, a valuable intellectual exercise, quite apart from what it accomplishes.

7. Dicotyledons and Monocotyledons

In considering the morphology of the angiospermous flower we have referred to the dicotyledonous type only. On the basis of comparative morphology of existing groups it is possible to trace a possible relationship between the Dicotyledons and Monocotyledons through the Ranales. Certain members of this order are comparable with Monocotyledons in anatomical characters and also in possessing only one cotyledon in their embryos. On this account they have been named Pseudo-Monocotyledons. Fossil remains of both groups, however, appear to be contemporaneous in geological history.

PART IV—THE LOWER CRYPTOGAMS

CHAPTER XVIII

LIVERWORTS AND MOSSES

1. The Group **Bryophyta** or **Muscineae** is divided into two Classes—the **Hepaticae** or *Liverworts*, and the **Musci** or *Mosses* (see p. 4). We shall consider *Pellia* as a type of the former, *Funaria* as a type of the latter.

A. PELLIA EPIPHYLLA

2. External Characters and General Life History

Pellia is found in various situations on damp ground. It is most frequently met with by the side of ditches, streams, or springs, sometimes submerged in the water. Each individual plant is a small, green, dorsiventral, dichotomously branching **thallus** (p. 6), from the under (ventral) surface of which numerous unicellular **rhizoids** are developed. The form of the thallus varies much under different conditions. The plants always grow in patches (Fig. 338), in which it is difficult to distinguish the individuals. If one of these individuals is separated out from the rest, it will be apparent that there is a striking resemblance to the prothallus of the fern. There are, however, clear differences. The thallus of *Pellia* is capable of growing and bifurcating indefinitely. Also, although it bears **antheridia** and **archegonia,** these sexual organs are borne on the upper (dorsal) surface of the thallus. As in the fern, they occur on the same plant. It is evident that the thallus of *Pellia* is the gametophyte, and is homologous with the fern prothallus. It is the product of a haploid, asexual spore and ultimately produces male and female gametes.

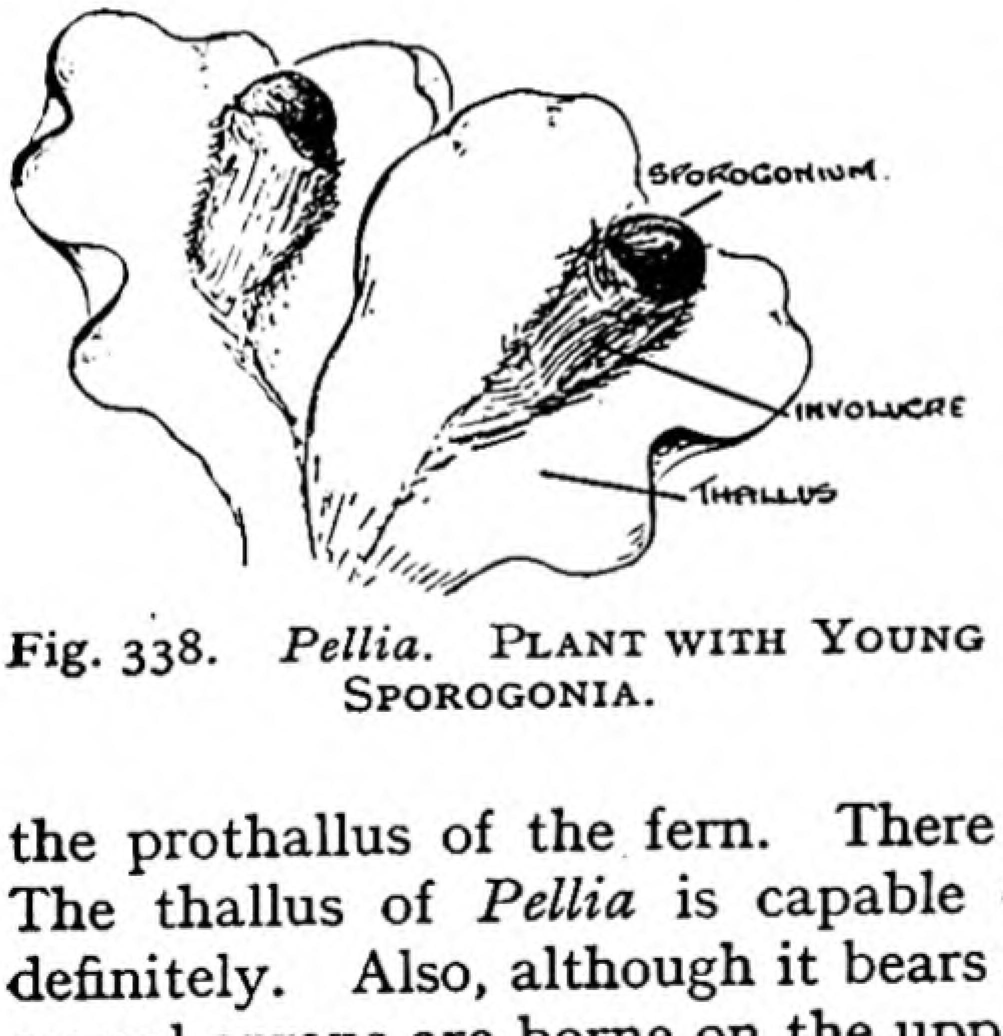

Fig. 338. *Pellia.* PLANT WITH YOUNG SPOROGONIA.

On the thallus, as in the fern, the sporophyte is eventually developed. It is called the **sporogonium** (Figs. 338, 345 and 346) and in its turn gives rise to the asexual spores. From the asexual spore a new gametophyte is produced.

The sporogonium is the homologue of the sporophyte of the higher plants. It consists of a capsule borne on a stalk or *seta*, at the lower end of which is an absorbing organ or *foot*, embedded in the tissue of the thallus. It thus shows only a rudimentary differentiation, and throughout its life it is parasitic on the gametophyte. It never becomes an independent plant, and in this respect differs from the fern sporophyte.

3. Structure of the Thallus

The thallus, as a rule, does not have a distinctly marked midrib. A transverse section (Fig. 339) shows that the thallus consists of several layers of cells in the middle and thins off to a single layer at the margins. These cells are parenchymatous and contain numerous chloroplasts and small oil-bodies. The chloroplasts are most abundant in the cells near the surface.

In some parts, more especially in the older thalli, the cell-walls may bear characteristic band-like thickenings. There are no stomata, no vascular tissues and no roots.

The unicellular **rhizoids** are tubular outgrowths from the cells of the lower surface of the thallus. They fix the plant on to the soil and also augment the lower absorptive surface of the thallus.

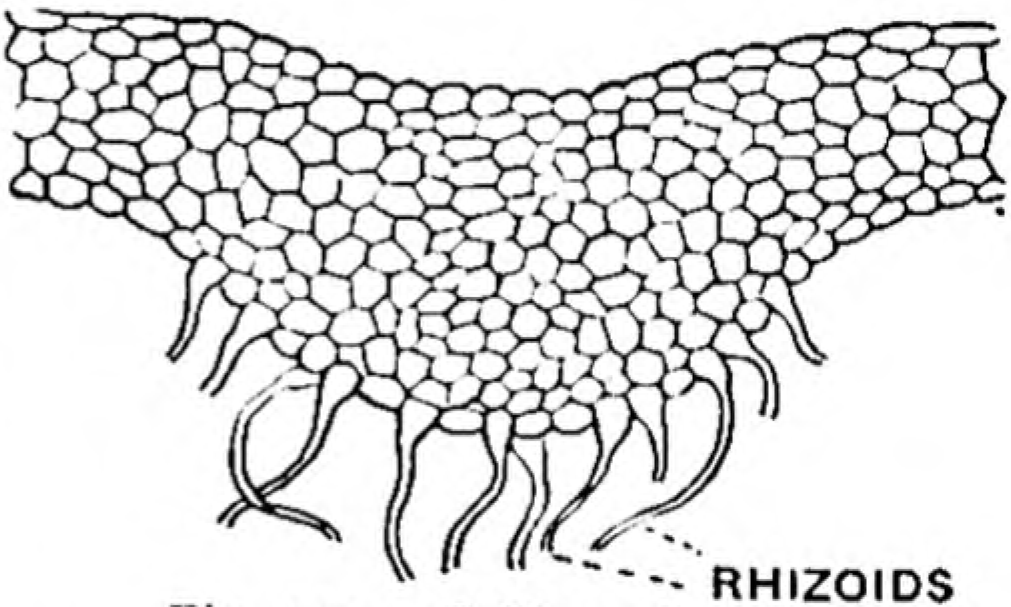

Fig. 339. *Pellia epiphylla.* Transverse section through central region of the thallus.

At the tip of each branch of the thallus there is a growing point with a single two-sided apical cell, from which segments are successively cut off. Owing to the more rapid growth of the marginal cells, the growing point becomes sunk in a depression (*cf.* prothallus in fern). In the process of branching, one of the segments cut off becomes a new apical cell. The cells of the lower surface near the growing point form short-lived glandular hairs, which secrete mucilage. This mucilage protects the growing point from desiccation.

4. The Antheridia

The antheridia make their appearance on the thallus about the end of April or beginning of May, and their development in each plant precedes that of the archegonia. Their position is indicated by a number of raised dots scattered over the thick central region of the dorsal surface (Fig. 340, A). A section of the thallus passing through one of these shows that the antheridium is a somewhat spherical body borne on a short multicellular **stalk**, and enclosed in a flask-shaped cavity which has an opening on the surface of the thallus (Figs. 340, A and 341). The wall of the antheridium consists of a single layer of cells, containing chloroplasts. Inside there is a mass of **spermatocytes**, each of which gives rise when liberated to a biciliate **spermatozoid** (Fig. 342, B).

In the development of the antheridium a cell grows out from the upper surface of the thallus, and is divided into transverse segments. The lower cells form the stalk; the terminal cell is divided into two by a longitudinal wall. In each cell thus formed two successive divisions by oblique longitudinal walls cut off the wall of the antheridium from the spermatogenous tissue. The latter divides up into small cubical spermatocytes, each of which gives rise to a short, spirally-coiled spermatozoid which consists mainly of nuclear material and bears two cilia at the more pointed anterior end. The flask-shaped cavity in which the antheridium is enclosed is formed by the growth of the surrounding tissue of the thallus.

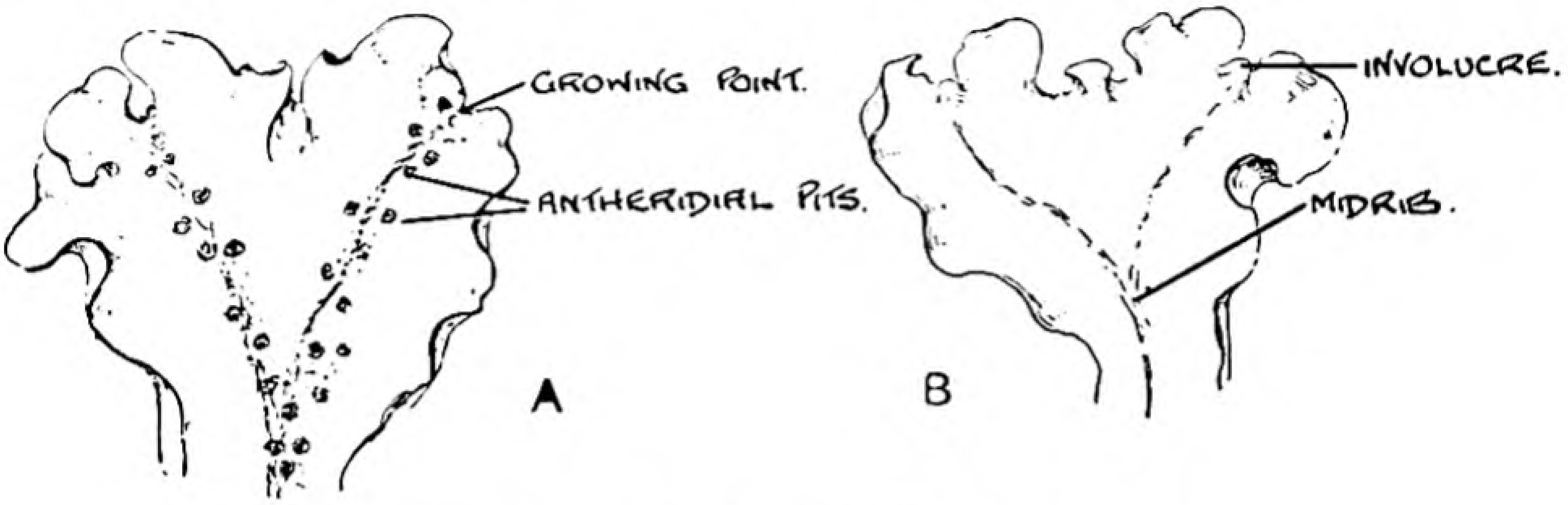

Fig. 340. *Pellia.* THALLUS.
A, Showing position of antheridia, and
B, of archegonia (under involucre).

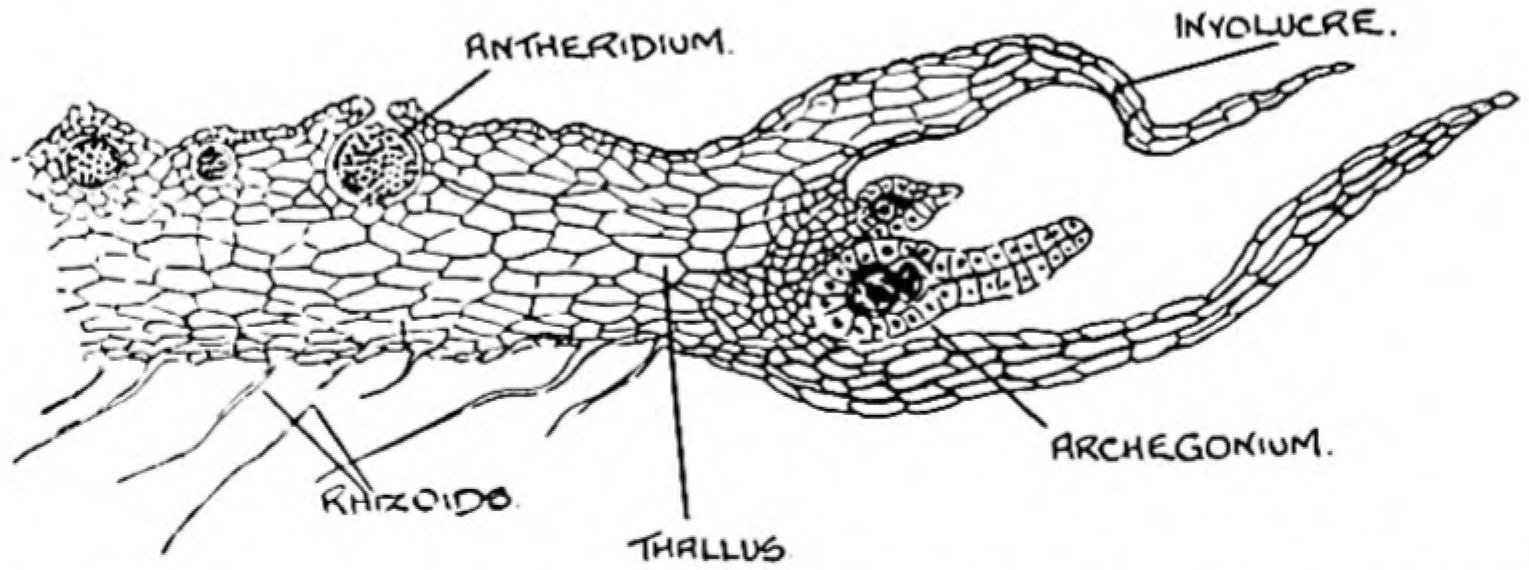

Fig. 341. *Pellia.* VERTICAL SECTION OF THALLUS THROUGH ANTHERIDIA AND ARCHEGONIA.

5. The Archegonia

The archegonia are developed in a group behind the growing point (Figs. 340, B, and 341). A growth of the tissue of the thallus, arising from behind the group, arches over and protects the archegonia. It is called the **involucre.** Each archegonium is borne on a short, stout stalk, and consists of a dilated **venter** and a long **neck**

(Fig. 342, C). The wall of the venter, when fully developed, consists, in *Pellia*, of two layers of cells. It contains the **oosphere** and a small **ventral canal-cell.** In the canal of the neck there is a row of **neck-canal-cells.**

The neck consists of about six longitudinal rows of cells surrounding the canal. The terminal cells, called **cap-cells**, are at first united, so that in the young archegonium the apex of the neck is closed. When the archegonium is mature the ventral canal-cell and the row of neck-canal-cells become disorganised, and are converted into mucilage, which absorbs water, forces open the cap-cells, and oozes out of the neck.

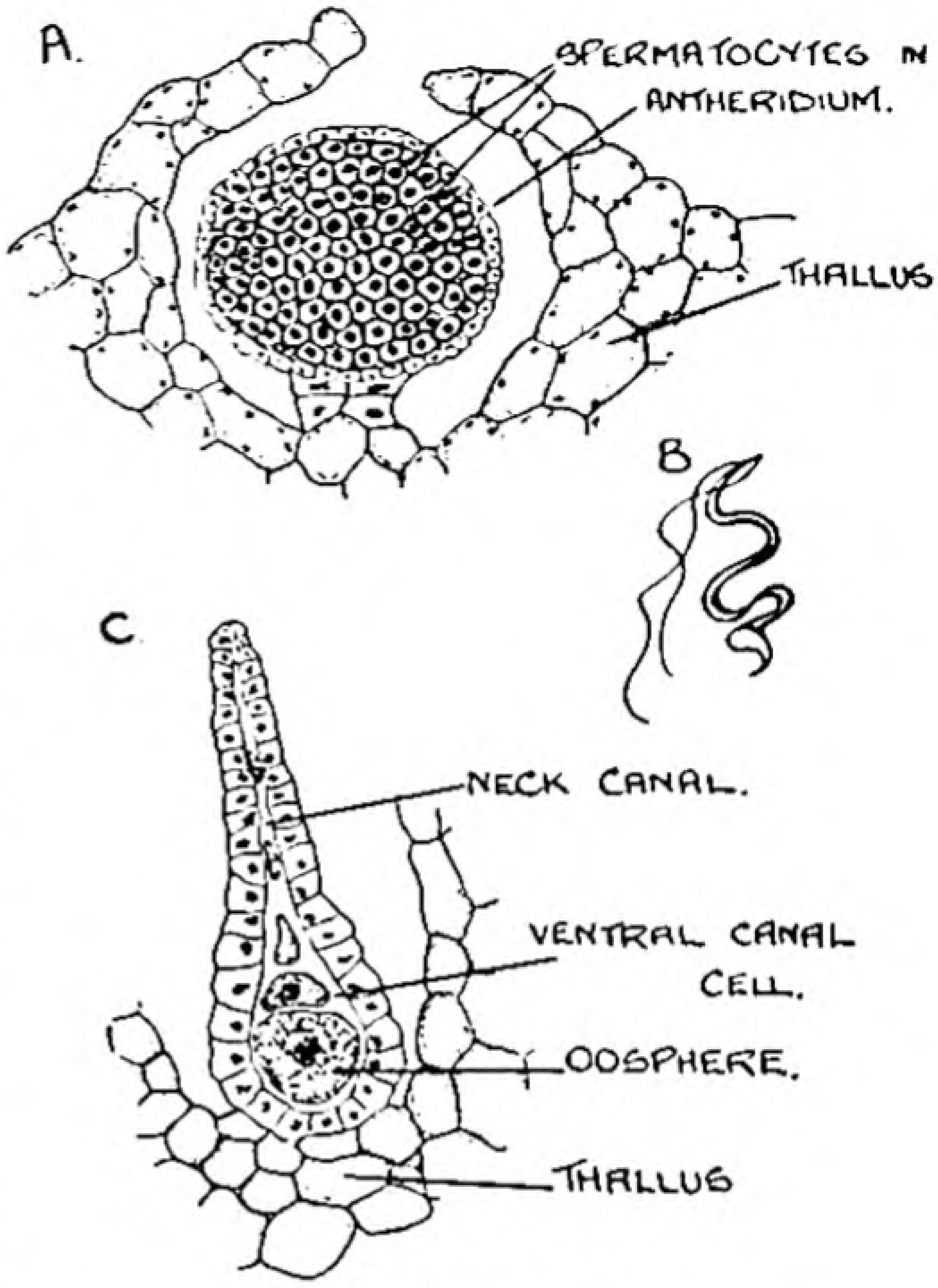

Fig. 342. *Pellia.*
A, Antheridium containing Spermatocytes; B, Spermatozoid; C, Longitudinal section, Archegonium.

The archegonium is developed as a protuberance from a single cell (Fig. 343). This grows out, and is cut off from a basal cell by a transverse wall. The basal cell undergoes a few divisions and forms the stalk. The other cell is the mother-cell of the archegonium. It is divided by three longitudinal walls into three *peripheral* cells and one *central* cell. The central cell overtops the peripheral cells, and its apical portion is cut off as the cap-cell, which afterwards by further division forms the cap-cells of the neck. The peripheral cells are further divided longitudinally into six, which are called *envelope-cells.*

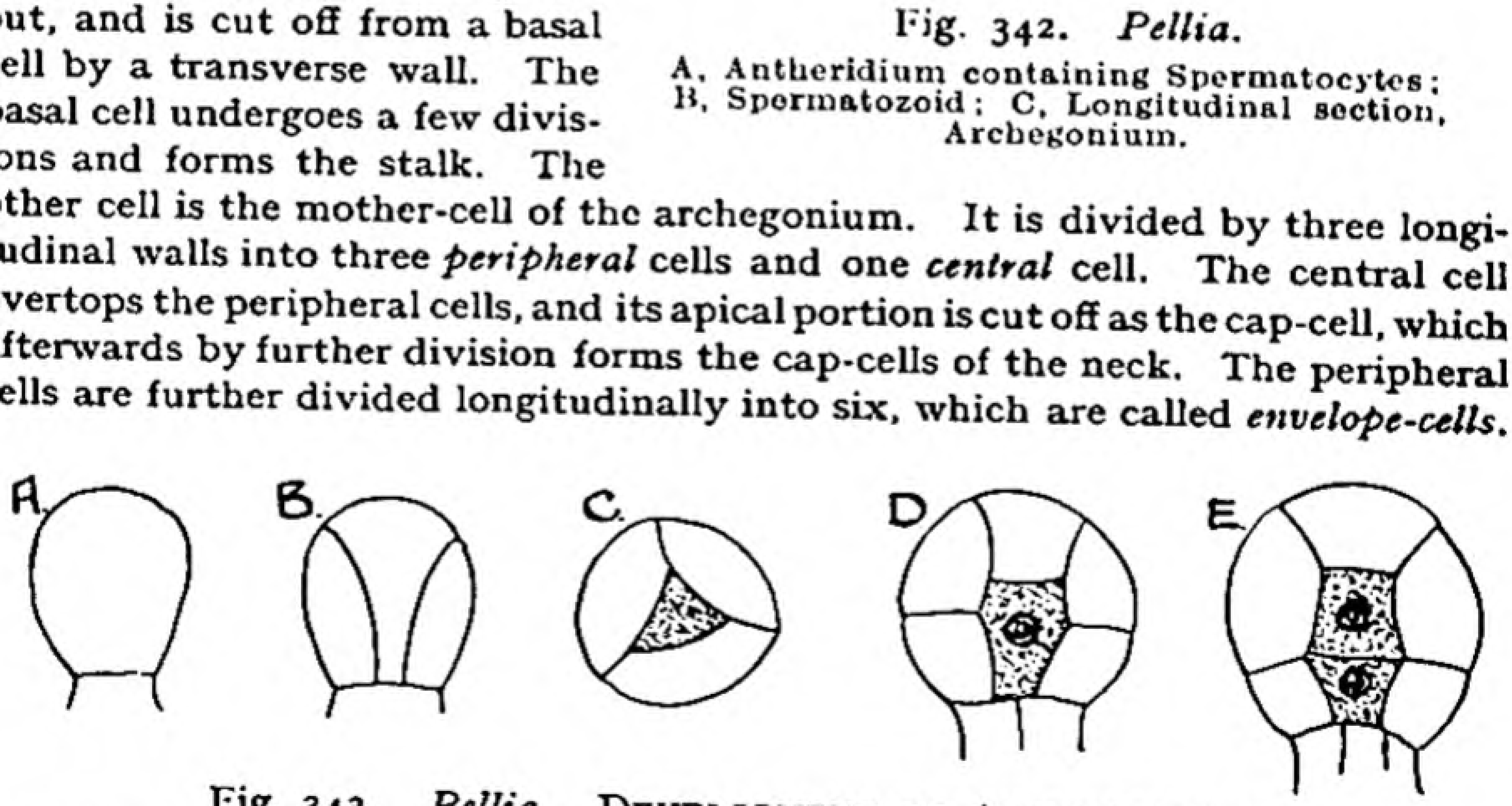

Fig. 343. *Pellia.* DEVELOPMENT OF ARCHEGONIUM.
A and B, Longitudinal section; C, Transverse section of B; D and E, Longitudinal section.

The six envelope-cells and the single central cell are then divided transversely into two storeys. The lower storey forms the venter; its envelope-cells further divide to form the wall; its central cell divides into oosphere and ventral canal-cell. The upper storey forms the neck; its central cell forms by division the row of neck-canal-cells.

6. Fertilisation and Development of Sporogonium

Fertilisation takes place in the presence of water. The antheridium bursts at the apex, and the spermatozoids are set free. They are attracted to the archegonia by some organic substance (apparently protein substances) present in the mucilage which oozes out of the neck.

The effects of fertilisation are not confined to the oospore. The venter of the archegonium continues to grow, and form an investment, called the **calyptra,** round the developing embryo (Fig. 345). Only one sporogonium is developed within each involucre. The other archegonia abort, and are frequently to be seen round the base of the developing calyptra.

The oospore is first divided by a transverse or basal wall into **epibasal** and **hypobasal cells.** The hypobasal cell in *Pellia* undergoes no further development, and the whole of the sporogonium is developed from the epibasal cell. It is divided transversely into two cells—an upper cell from which the capsule of the sporogonium is developed, and a lower cell which gives rise to the stalk or seta.

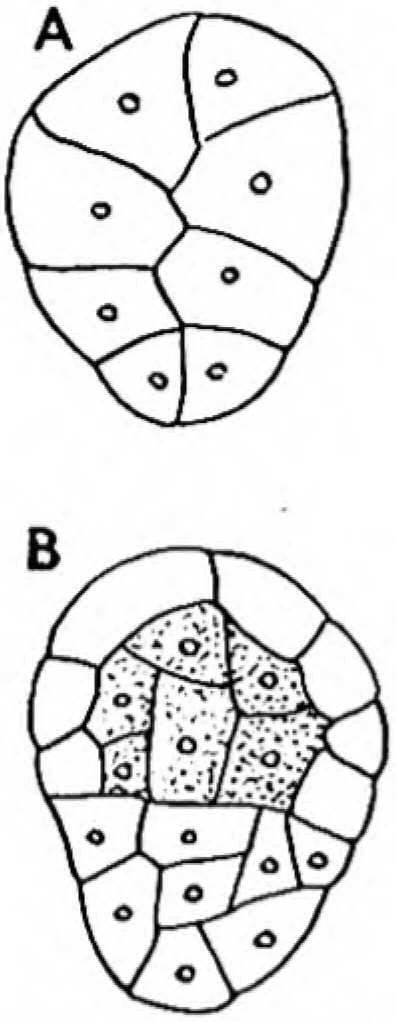

Fig. 344. *Pellia.* EARLY STAGES IN DEVELOPMENT OF SPOROGONIUM.

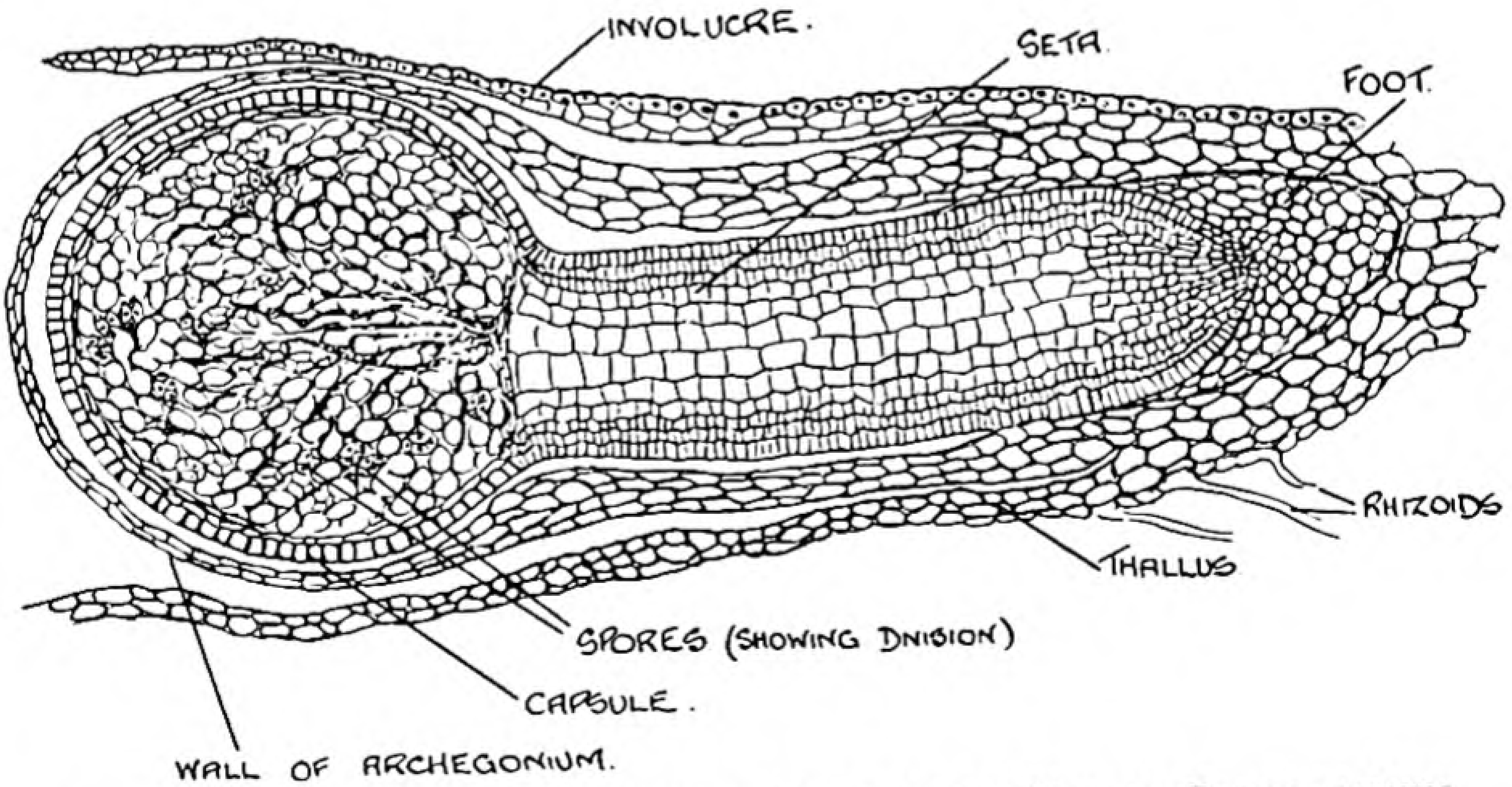

Fig. 345. *Pellia.* LONGITUDINAL SECTION OF YOUNG SPOROGONIUM.

Further divisions follow in both (Fig. 344). The lower end of the seta develops into a bulbous absorbing organ, the foot, embedded in the tissue of the thallus (Fig. 345). In the capsule a wall of two layers of cells is cut off from a central mass. The latter differentiates into spore-mother-cells and others which remain sterile. Some of these become long and slender, and a double-spiral thickening is developed on their walls. They are called *elaters*. The others form a central tuft of elater-like cells attached to the base of the capsule, called an *elaterophore* (Fig. 345).

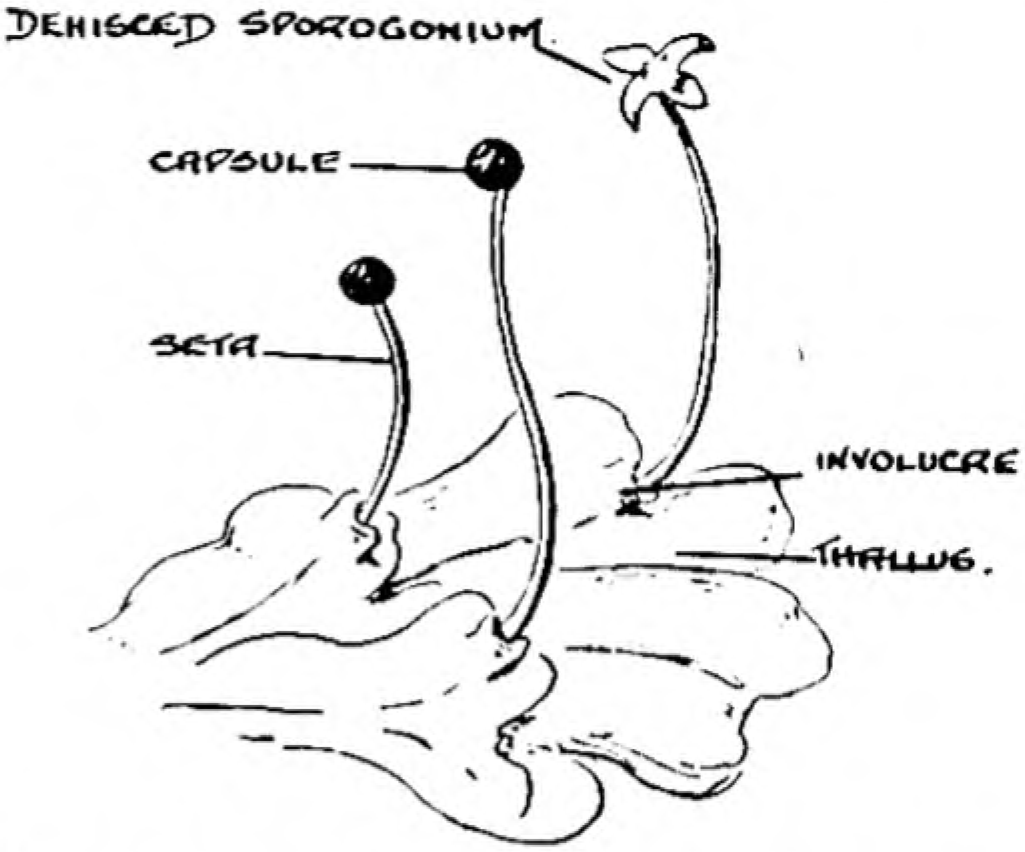

Fig. 346. *Pellia*. PLANT WITH RIPE SPOROGONIA.

The spore-mother-cells are four-lobed. The original single diploid nucleus of each spore-mother-cell divides meiotically. A nucleus passes into each lobe to become the haploid nucleus of a spore.

The outer layer of the wall of the mature capsule consists of cells whose radial (anticlinal) walls possess rod-like thickenings. Further, the cell-walls of the second layer are somewhat reticulately thickened.

The development of the sporogonium in *Pellia* is not completed till nearly a year after the fertilisation of the oosphere. Early in the following year the heads of the young sporogonia protrude from under the involucres, but they are still enclosed in the calyptras (Figs. 338 and 345). Generally about four months later a very rapid elongation of the stalk causes the rupture of the calyptra, and raises the glossy black capsule into the air. By this time the thallus has recommenced its growth, and has already begun to form antheridia and archegonia for the current year (Fig. 346).

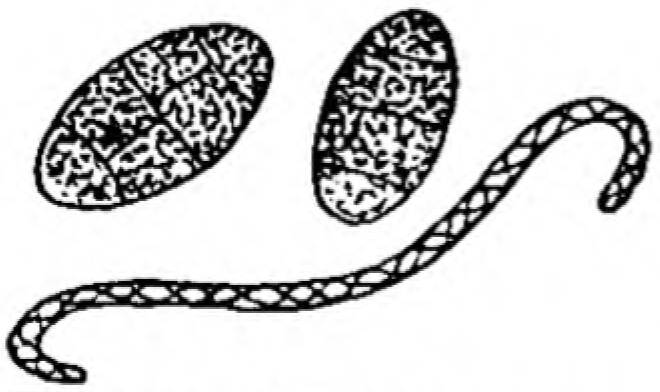

Fig. 347. TWO SPORES AND AN ELATER OF *Pellia*.

7. Germination of the Spores

The spores of *Pellia* (Fig. 347) are exceptional in that they undergo division while still inside the capsule. The result of division is the formation of a small ellipsoidal mass of cells which are rich in protoplasm and chloroplasts, still enclosed within the spore-wall.

These multicellular spores are first set free in the cavity of the capsule by the gradual breaking down of the wall of the spore-mother-cell, beginning at the tips of the lobes and continuing backwards until the thickened, middle, constricted region is left.

The dehiscence of the capsule soon follows. It is brought about as the result of loss of water by the wall-cells causing unequal shrinkage of the outer and inner surfaces, as in the fibrous layer of an anther. The wall separates into four valves which become reflexed. Meanwhile the elaters as they dry coil and twist, and those of the elaterophore flick to and fro, thus assisting in the liberation of the spores. After the spores are shed the elaterophore persists as a tuft.

Growth of the spore continues after it is liberated. At one end a small rhizoid is usually developed. At the other end an apical cell of a *Pellia* thallus arises laterally and proceeds to divide. The apical cell is two-sided and cuts off segments parallel to its two sides and base. These further divide to build up the tissue of the thallus.

The life history of *Pellia* is represented graphically in Fig. 348.

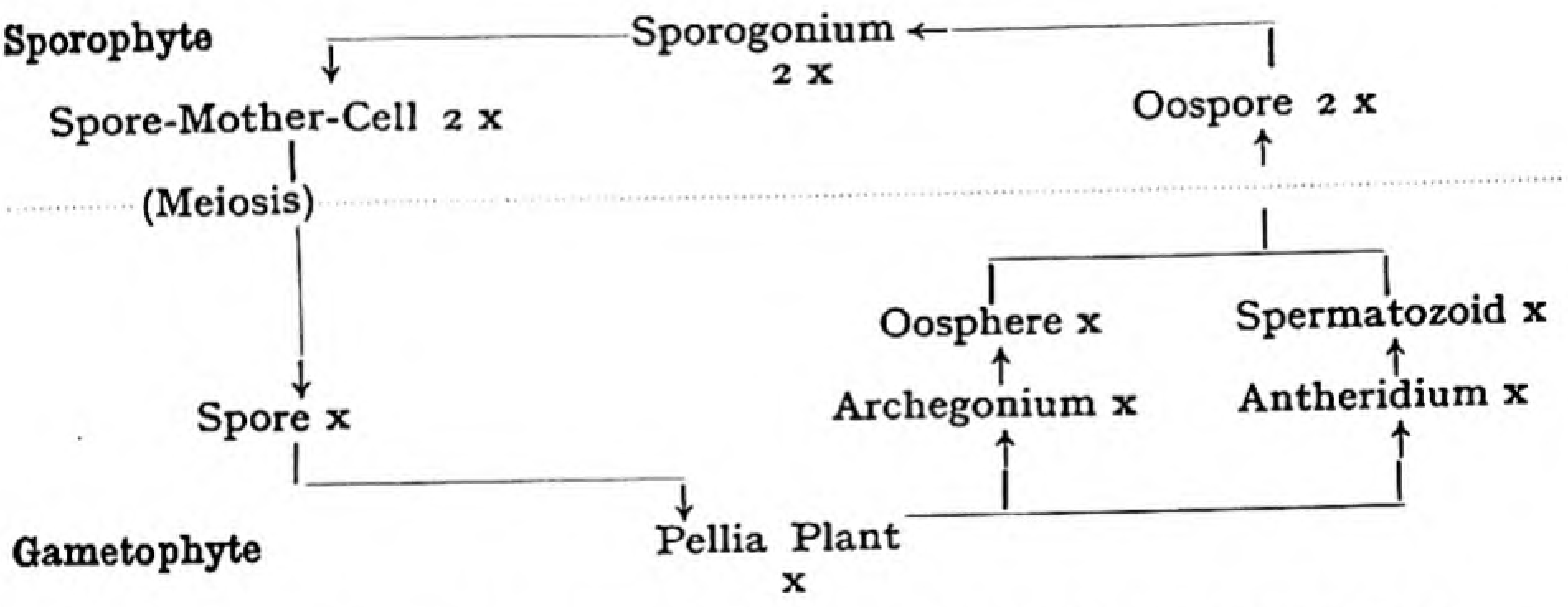

Fig. 348. LIFE HISTORY OF *Pellia*, GRAPHICALLY REPRESENTED.
(x = the haploid number of chromosomes.)

8. Vegetative Reproduction

Many liverworts (e.g. *Aneura, Lunularia, Marchantia,* etc.) also reproduce vegetatively by means of gemmae. These are generally produced in small cup-shaped outgrowths—gemma cups—which are situated on the upper surface of the thallus. Each gemma arises by repeated division of an epidermal cell and consists of a flat, multicellular, disc-like, stalked body, green in colour. These, when separated from the parent plant, develop into new thalli.

B. FUNARIA HYGROMETRICA

9. External Characters (Fig. 349)

Funaria is a common moss which grows in dense tufts or patches on the surface of the ground, often on the top of walls. It is one of the first of the mosses to recolonise burnt patches in woodland areas. The plants are small, being scarcely half an inch in height. They are differentiated into stem and leaf, but there is *no true root*. The dark-coloured base of the shoot gives off numerous slender, brown *multicellular* **rhizoids**, which pass down into the soil. The leaves are simple and more or less ovate. They show a distinct midrib, and have a $\frac{3}{8}$ spiral phyllotaxis. There is comparatively little branching which is lateral and not axillary; the branches are given off beneath the leaves.

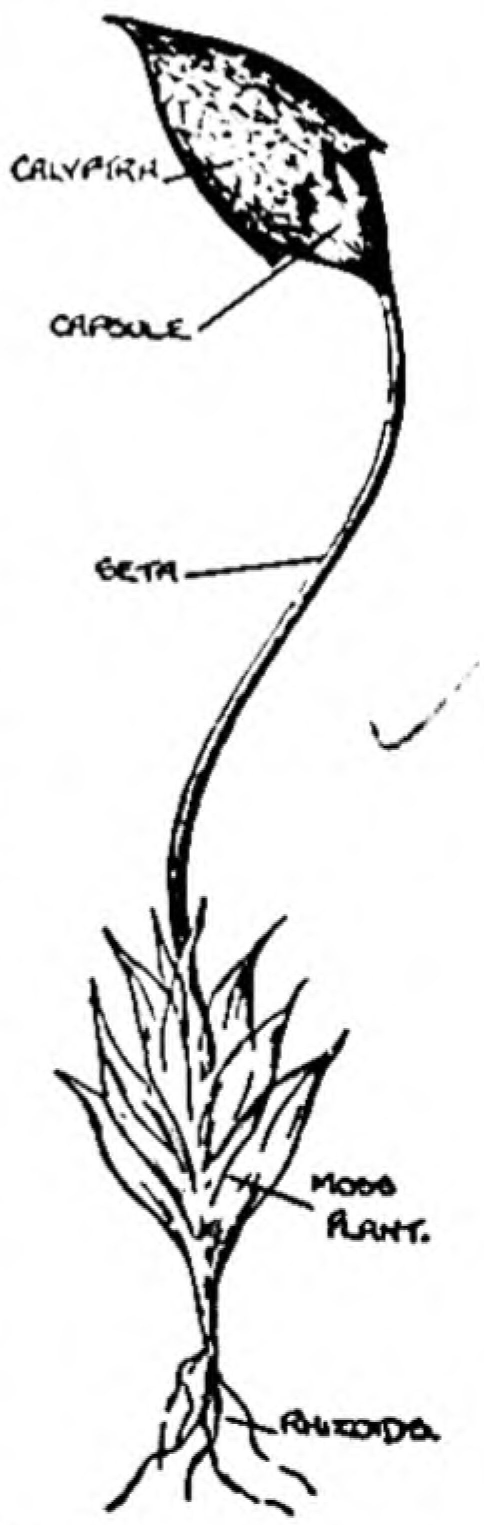

Fig. 349. *Funaria.* PLANT WITH SPOROGONIUM.

10. General Life History

The plant, as in the Hepaticae, is the **gametophyte**, but is much more highly differentiated. In the mosses the gametophyte attains a high degree of development. The **antheridia** and **archegonia** are borne at the apices of two branches of a single shoot. *Funaria* is monoecious. The antheridia terminate the primary axis, which, however, becomes the shorter one. They can be distinguished by the rosette-like arrangement of the leaves which are spreading and form a *perichaetium*. The central leaves of the rosette are often reddish in colour. The shoots bearing archegonia spring from the bases of the male shoots, but soon overtop them. The leaves at the apex are usually erect and closely folded.

It should be carefully noticed that the stem and leaves of the moss are not homologous with, but only analogous to, the stem and leaves of the fern-plant; they belong to different generations.

In mosses, as in Hepaticae, the sporophyte generation is represented by a **sporogonium** derived from the fertilised ovum. The sporogonium (Fig. 349) is rather more highly differentiated, but, like that of *Pellia*, consists of a **capsule, seta,** and **foot.**

The asexually produced spore gives rise to a **protonema** (Fig. 356), which, however, is a much larger and longer-lived structure than that of Hepaticae. It is a much-branched filament bearing an external resemblance to a green Alga. The branches are obliquely septate and the cells contain numerous chloroplasts. Finer, brown branches pass down into the soil, and act as rhizoids. The **moss-plant** is developed on the protonema as a lateral bud. The protonema continues to grow for some time, and produces numerous plants. Thus, as in Hepaticae, the development of the gametophyte from the asexual spore is *indirect*.

Funaria has great powers of **vegetative reproduction.** Protonemata may be produced from any part—rhizoids, stem, leaf, and even from the sporogonium. The last case is an instance of **apospory** (p. 271). Some mosses (not *Funaria*) form multicellular *gemmae*.

11. Structure of the Stem

The outermost layer of cells, or epidermis, of the stem is marked off from a many-layered cortical region, surrounding a central strand of elongated thin-walled cells. The cells of the cortex contain chloroplasts, and in the outer region their walls are thickened. The central strand is a conducting tissue. In some mosses, such as *Polytrichum* (Fig. 350), but not in *Funaria*, the conducting strand shows a further differentiation of a central region of thick-walled cells surrounded by a region of thin-walled cells.

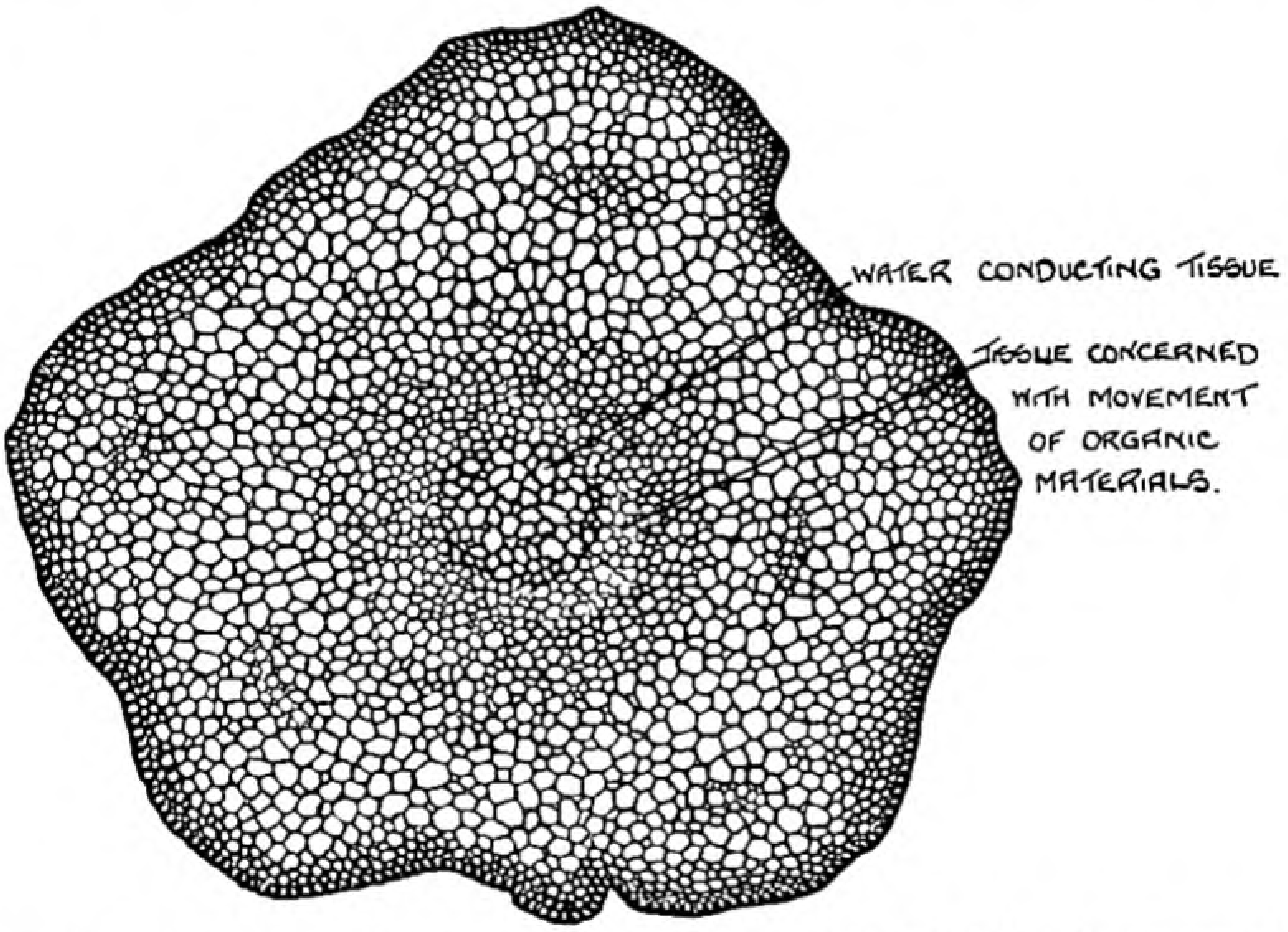

Fig. 350. TRANSVERSE SECTION, STEM OF MOSS (*Polytrichum*), SHOWING SOME DIFFERENTIATION OF CONDUCTING TISSUES IN A GAMETOPHYTE.

The growth of the stem in mosses is effected by a three-sided apical cell like that of the fern. The segments cut off from it divide into inner and outer halves, of which the former give rise to the central conducting tissue. Each outer half is divided into upper and lower parts. The upper part protrudes as a two-sided apical cell, and develops into a leaf. The lower part forms the cortical tissue of an internode. If branching occurs, the branch is formed from this lower part.

12. Structure of the Leaf

Except at the midrib the leaf consists of a single layer of cells containing chloroplasts. This is the **assimilating tissue.** The leaf is thickened at the midrib, which contains a strand of thin-walled conducting cells like those of the stem, but not continuous with them.

13. The Antheridia (Figs. 351 and 352, A)

The antheridia are club-shaped bodies, borne on stout multicellular stalks. The wall of each consists of a single layer of cells, enclosing numerous **spermatocytes.** On the access of water the antheridium bursts at the apex, and the spermatocytes are liberated as a mass of cells which then breaks up into separate **spermatozoids** (Fig. 352, B). They are biciliate like those of Hepaticae.

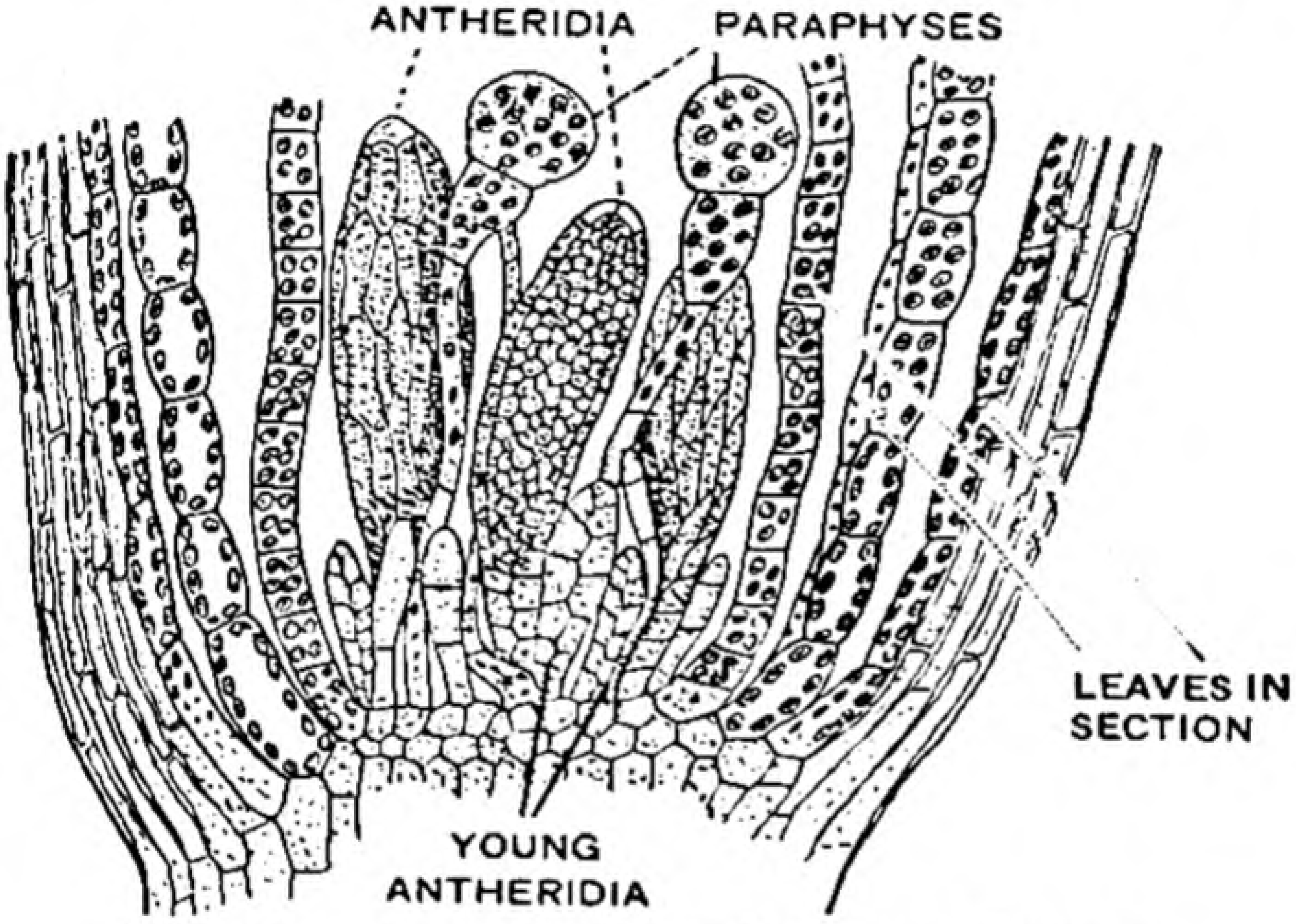

Fig. 351. Apex of Male Shoot of *Funaria*. (Longitudinal section.)

The antheridia are developed from single cells at the apex of the shoot, including even the apical cell. The cell grows out, and is divided into two. The lower cell forms the stalk. The upper grows like a two-sided apical cell, and gives off two series of segments, which are divided into central cells, from which the spermatocytes are developed, and peripheral cells forming the wall. This mode of apical growth, which is characteristic of mosses, is unusual.

14. The Archegonium (Fig. 352, C)

The archegonium is like that of Hepaticae; but the stalk is more strongly developed. The wall of the venter consists of two layers of cells. There is a long twisted neck, consisting of six longitudinal rows of cells, surrounding the central canal.

The archegonium (Fig. 353) is developed from a single cell, which grows out, and divides into two. The *lower cell* forms the stalk. The *upper cell* functions as a three-sided apical cell. It shows continued growth, and gives off segments forming, after further division, tiers of cells, each tier consisting of a central cell and surrounding 3 peripheral cells. The lowest central cell forms the oosphere and ventral canal-cell; the other central cells form the neck-canal-cells. The peripheral cells form the cells of the neck and venter. Here also the continued apical growth is highly remarkable.

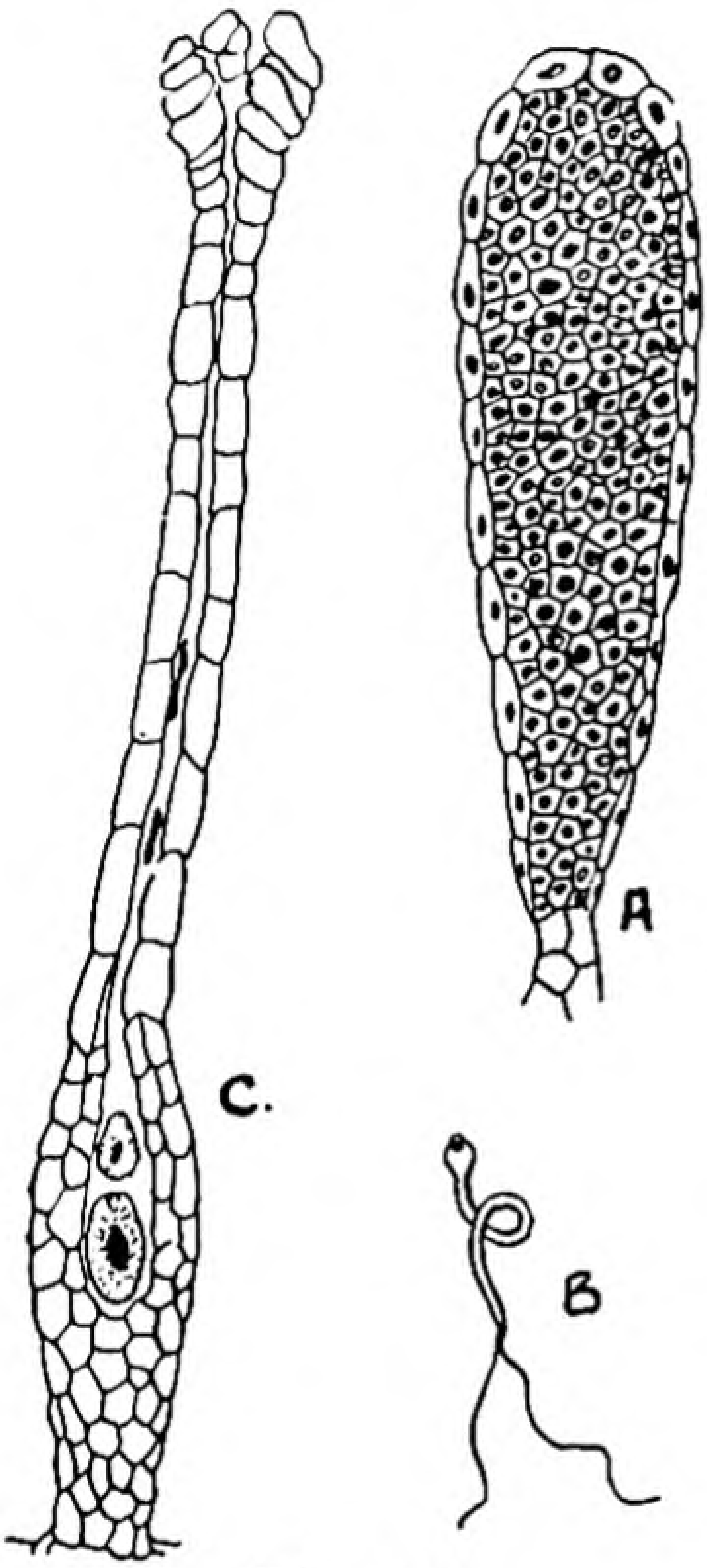

Fig. 352.
A, Antheridium; B, Spermatozoid; C, Archegonium.

15. Fertilisation

Fertilisation is effected in the usual way. The spermatozoids swim to the archegonia when the plants are wet. The attracting substance here seems to be cane-sugar. The oospore develops into the sporogonium.

16. Structure of Sporogonium

The sporogonium, representing the sporophyte generation, consists of foot, seta, and capsule. The **foot** (Fig. 355, E) is a small conical structure which buries itself in the apex of the female shoot, and serves for the absorption of nutriment. It is invested by the remains of the lower half of the archegonium, which is ruptured during the development of the sporogonium. The **seta** is a long slender structure of a reddish colour. It has an epidermis, a thick-walled cortex, and a conducting strand like that of the moss-plant.

The **capsule** (Fig. 354) is a pear-shaped structure. Its solid basal region is called the **apophysis.** The epidermis of the apophysis has true stomata. At each end of the pore the wall between the two original guard-cells breaks down, so that the pore seems to be surrounded by a single ring-shaped cell. The parenchymatous cells beneath the epidermis contain chloroplasts. The conducting strand of the seta is continued into the apophysis. The sporogonium can synthesise carbohydrates, and inorganic solutions are absorbed by the foot. Therefore the sporophyte is only a partial parasite on the gametophyte.

The **wall** of the capsule consists of several layers of cells; the inner layers contain chloroplasts. Internal to this is a large **air-space** traversed by delicate strands of cells. Next comes the **spore-sac,** surrounding a sterile central column, the **columella.** The outer wall of the spore-sac consists of two or three layers of cells. The inner wall lies next the columella.

At the apex of the capsule is a lid, the **operculum,** which separates off when the capsule dehisces. The dehiscence is effected by the rupture of a ring of cuticularised epidermal cells, the **annulus,** round the base of the operculum, immediately above the upper end of the spore-sac. When the operculum comes away a number of yellow, thickened, tooth-like structures, constituting the **peristome,** project. These are hygroscopic, and allow the spores to escape only when the air is dry. In *Funaria* there are two rows of peristome teeth (outer and inner). They represent the outer and inner thickened and cuticularised regions of the walls of a plate of cells which have otherwise broken down. The sixteen outer teeth of the peristome are joined at their tips by a small disc of tissue. The apex of the capsule is covered by a membranous cap, the **calyptra** (see Fig. 354, E), representing the upper portion of the ruptured archegonium.

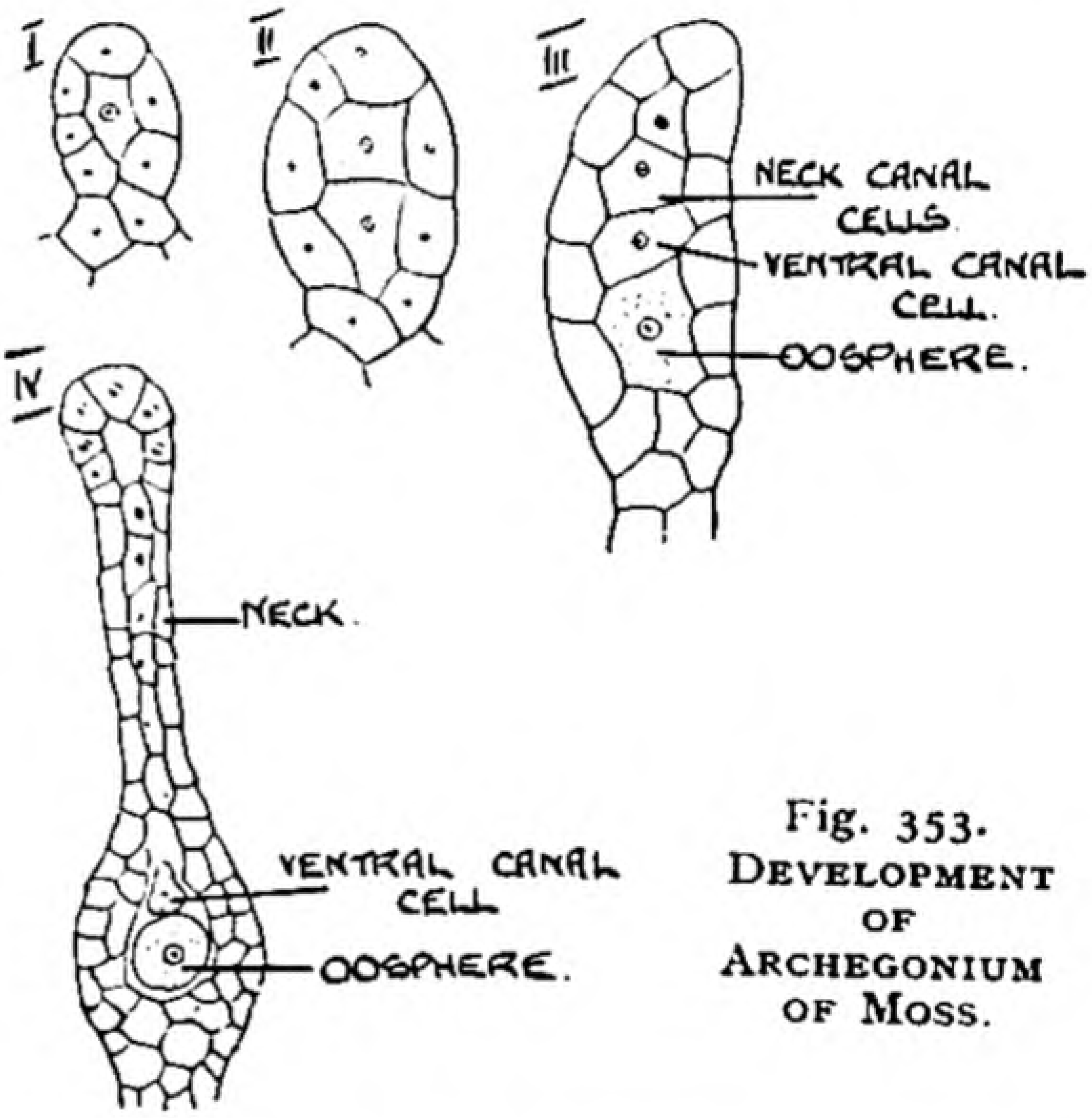

Fig. 353. Development of Archegonium of Moss.

17. Development of Sporogonium (Fig. 355)

The oospore is first divided by a **basal wall** into **hypo-** and **epi-basal cells.** By further division a two-sided apical cell is formed at each end. The two rows of segments cut off from the apical cell at the hypobasal end form the foot (A). The epibasal half also forms two rows of segments (A, B). The segments are divided into outer and inner halves (A, C). In the region of the seta the inner halves form the central conducting tissue; the outer halves the cortical tissue. In the region of the capsule, which is not distinctly marked off from the seta till the embryo has elongated considerably, the outer halves constitute the **amphithecium**; the inner halves the **endothecium** (D).

The **archesporium** is the *outermost layer* of the endothecium, the rest of the endothecium forming the columella. Everything outside the sporogenous tissue, including the outer wall of the spore-sac, is derived from the amphithecium. The operculum slowly differentiates, and the innermost layer of the amphithecium over the region covered by the operculum gives rise to the peristome. The **spores** are developed from the mother-cells in the usual way. There are no elaters.

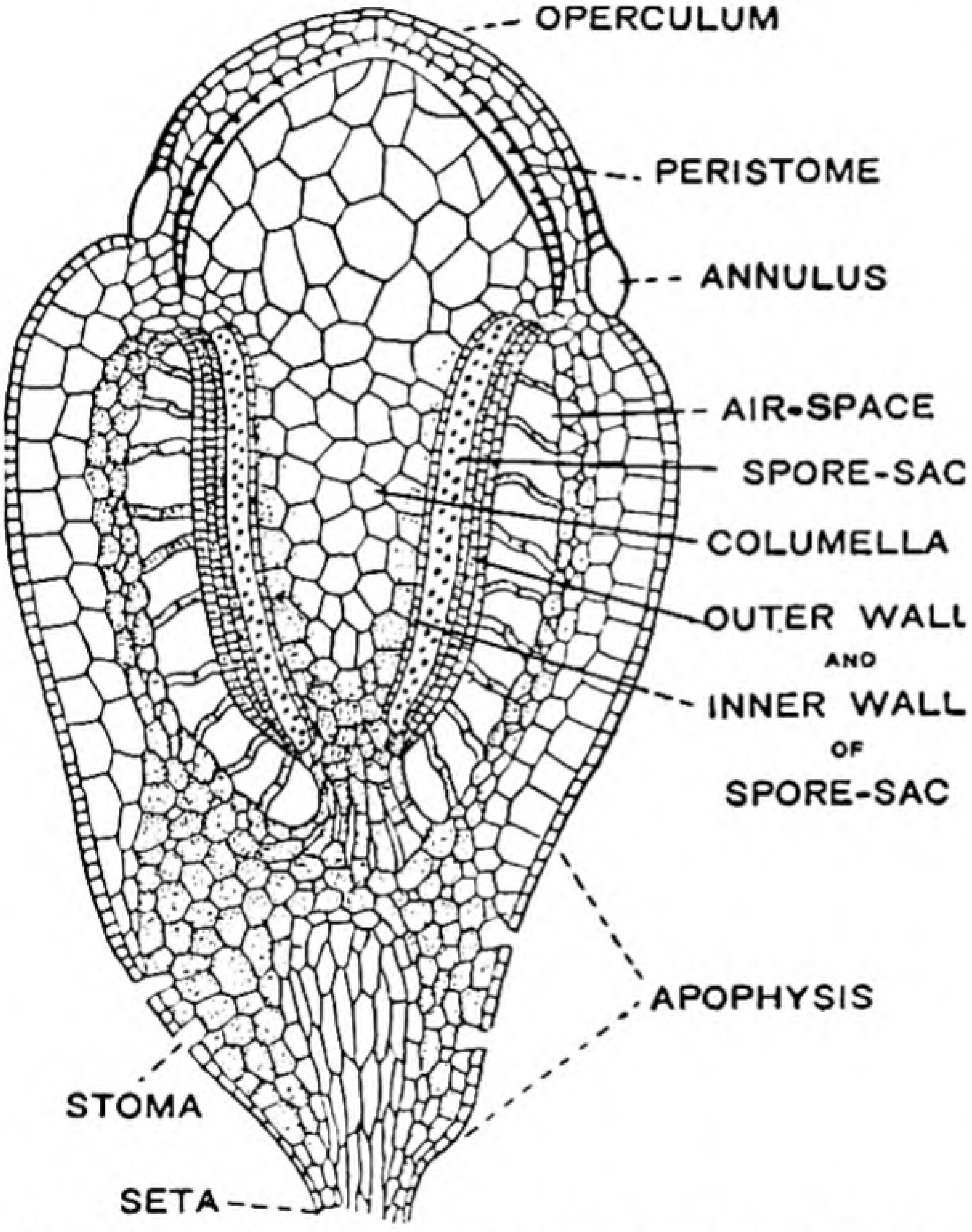

Fig. 354. Longitudinal Section of Capsule of *Funaria* (semi-diagrammatic).

18. Germination of the Spore (Fig. 356)

When the spore germinates a germ-tube grows out at one end to form a rhizoid. An outgrowth at the other end of the spore develops into the protonema.

19. The Young Moss-plant (Fig. 356)

This arises as a bud from a cell of the protonema close to a septum. In this protuberance three oblique divisions appear, and these separate the pyramidal apical cell of the young plant from those which give rise to the first leaf and the first rhizoid. Further leaves arise, one from each segment of the apical cell. The leaves are therefore arranged in three orthostichies. This is not always evident because of a slight twisting in the growth of the axis. This twisting ensures a fuller exposure of leaves to light in that the upper leaves of the same orthostichy do not shade the lower ones. If branching occurs, the apical cell of the branch arises in the lower half of a leaf-segment. The life history may be represented graphically as in Fig. 348, for *Pellia*, by substituting " moss-plant " for " *Pellia* plant."

20. Summary and Conclusions

Thus, in the Bryophyta, there is a distinct alternation of generations. The gametophyte is the haploid plant, and includes the protonema; the sporophyte generation is represented by a diploid sporogonium parasitic or semi-parasitic on the gametophyte. The relative importance of the two generations has been reversed as compared with what we find in Vascular Cryptogams and Seed Plants. The sporophyte is little more than a sporogenous capsule; there are no distinct sporangia. A seta elevates the capsule, and a foot absorbs nourishment.

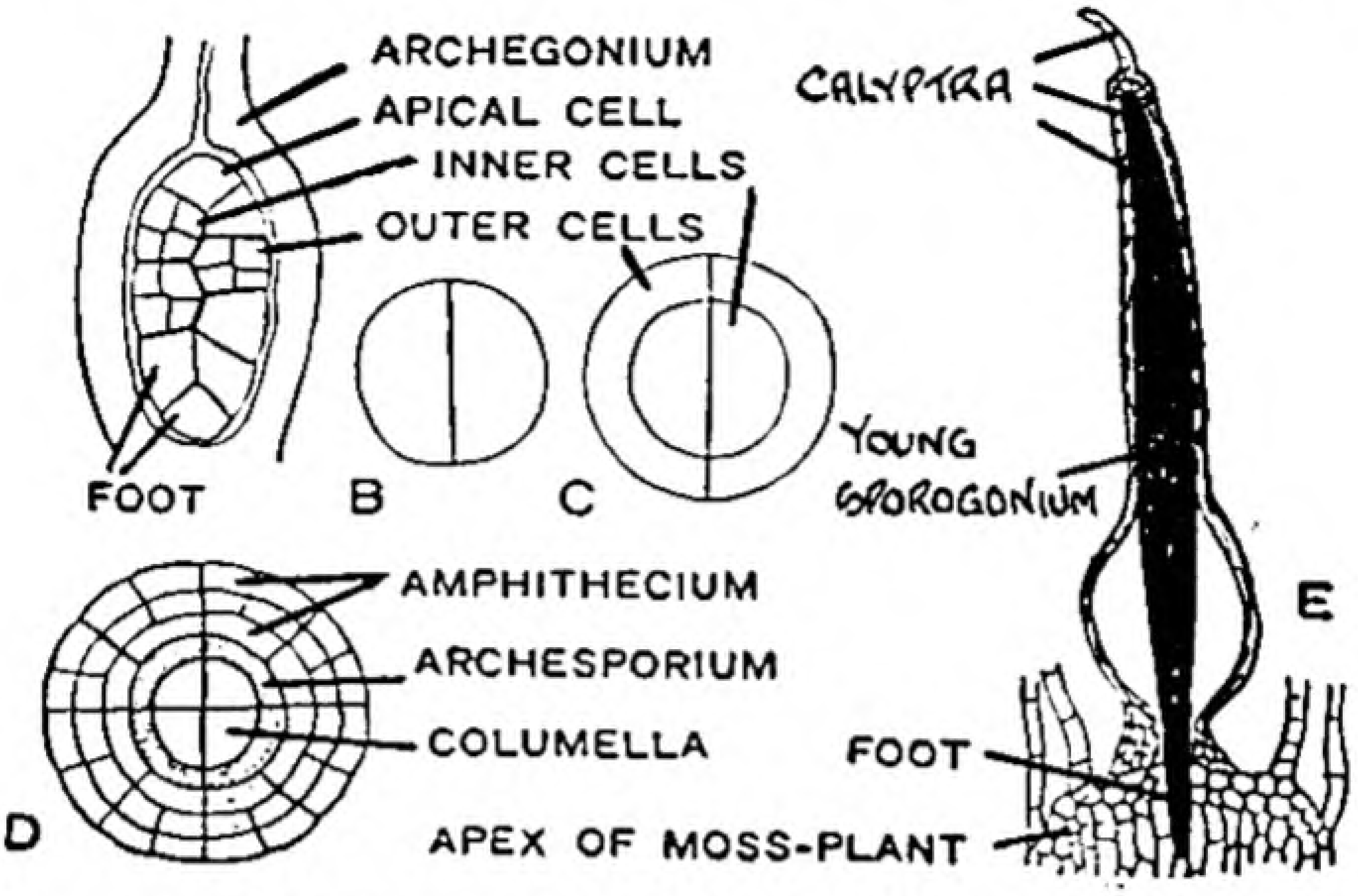
ARCHEGONIUM
APICAL CELL
INNER CELLS
OUTER CELLS
FOOT
B
C
CALYPTRA
YOUNG SPOROGONIUM
E
AMPHITHECIUM
ARCHESPORIUM
COLUMELLA
FOOT
D
APEX OF MOSS-PLANT

Fig. 355. DEVELOPMENT OF SPOROGONIUM OF *Funaria*.
B, C, D, Transverse section; D, In region of Capsule.

It is only in some liverworts that the plant-body is a thallus; in many it is differentiated into stem and leaves. In liverworts there is no filamentous protonema, elaters are usually present in the capsule, but there is no columella. In mosses the protonema is well developed; there is a columella in the capsule, but no elaters.

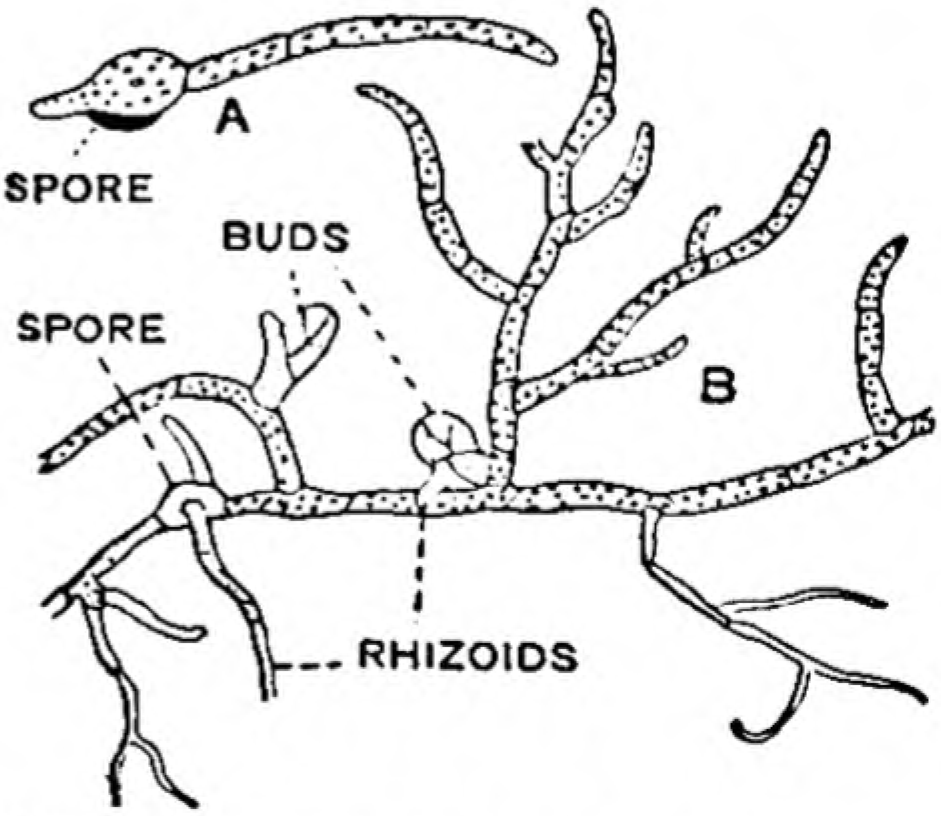
A
SPORE
BUDS
SPORE
B
RHIZOIDS

Fig. 356. A, GERMINATING SPORE; B, PROTONEMA OF *Funaria*.

Antheridia and archegonia are the characteristic sexual organs of the Bryophyta and Pteridophyta. For this reason the two groups are together spoken of as the *Archegoniatae*.

21. Relationship of Bryophyta and Pteridophyta

A derivation of the Pteridophyta from the Bryophyta does not appear to be possible. The question of relationship is bound up with that of organisation of the sporophyte, and it is difficult to see how the dependent sporogonium of the Bryophyta can have given rise to the highly differentiated sporophyte of the Pteridophyta. The two groups are comparable in their alternation of generations, the similarity in the general course of the life history, the character of the sexual organs and the development of the spores. But if they are to be related at all, a common ancestor must be sought for them among the Algae. Such a common ancestor is unknown. Fossil Bryophyta found in the Tertiary period closely resemble existing forms. The liverworts appear to be more ancient in that their remains are occasionally met with in Carboniferous strata.

CHAPTER XIX

THE ALGAE

1. General Characters

The Algae constitute one of the two important Classes into which the Thallophyta are subdivided. They are for the most part aquatic plants and there are many freshwater forms, but the great majority live in the sea, and constitute the assemblage of organisms called the marine Algae or seaweeds. Many of the lower forms are unicellular. In the higher forms the vegetative body is often a multicellular thallus. This may take various forms, e.g. a hollow sphere, a flat plate, a filament, an aggregation of filaments or a highly organised thallus with specialised tissues. In the multicellular types the same cells may fulfil both vegetative and reproductive functions, or special reproductive cells or organs may be developed.

In essential points the processes of nutrition resemble those of the ordinary green plant, but differ in detail (see p. 145). All the Algae contain chlorophyll, but, in many, the green colour of the plastids is masked by the presence of other pigments. These are chiefly a yellow pigment (fucoxanthin) in the Brown Algae, a red pigment (phycoerythrin), and a blue pigment (phycocyanin). The differences in colour are correlated with important differences in development and life history—hence the convenient division of the Algae into Green (Chlorophyceae), Brown (Phaeophyceae), Red (Rhodophyceae), and Blue-green (Cyanophyceae or Myxophyceae). The Brown and Red Algae are mostly marine.

2. Reproduction

While some of the lower Algae have only a vegetative method of reproduction by cell-division, in the higher Algae both sexual and asexual reproduction are of general occurrence, often in addition to vegetative reproduction.

There is usually no regular alternation of sexual or asexual reproduction. Frequently several generations of asexual plants occur before the appearance of a generation bearing sexual organs, whilst sometimes both sexual and asexual reproductive organs occur on the same plant. There is little doubt that external conditions play an important part in determining the onset of both asexual and sexual reproduction.

3. Asexual Reproduction

The spores may be special non-motile cells, but frequently they are naked protoplasmic bodies (protoplasts) which move by means of cilia, and are called **zoospores**; in this case they are formed from the contents of a mother-cell.

4. Sexual Reproduction

The **gametes** and the **gametangia,** *i.e.* the organs producing the gametes, may or may not be differentiated into male and female. If the sexual process is a conjugation of exactly similar gametes it is said to be **isogamous**; if of similar gametes of different size (micro- and macro-gametes) it is anisogamous; in both cases the **zygote** formed is termed a **zygospore.** If it is the fertilisation of an oosphere by a male gamete it is **heterogamous** (as in higher types) and the zygote is an **oospore.** This applies especially to the Green and Brown Algae; in the Red Algae the reproductive processes are of a very specialised type.

The zygospore or oospore may develop into a new plant either directly or after a period of rest, but it may form a number of spores by division or give rise to a small body in which they are formed.

5. Alternation of Generations

In the Algae, as in Thallophyta generally, there is no regular alternation of generations comparable with that found in the higher plants. Even in cases where the life history includes two forms of plant (gametophyte and sporophyte), these forms do not as a rule alternate regularly, and are not necessarily equivalent to the two generations in the higher plants.

We have seen that, in the higher plants, the sporophyte is diploid, while the gametophyte is haploid, the phenomenon of the doubling and the halving of a chromosome number being associated in a definite way with the alternation of generations. Attempts have been made to discover whether anything similar occurs among the Thallophytes. In many Algae meiosis has been demonstrated, but comparison of different Algae shows that it does not occur always at the same point in the life history. Sometimes it takes place at the first division of the zygote, e.g. *Spirogyra*; in this case the plant is haploid; but it may take place, as in *Fucus*, during the formation of the sexual cells, in which case the plant is diploid. It is, however, an interesting fact that in *Dictyota*, one of the Brown Algae, a sexual plant with the haploid number of chromosomes regularly alternates with an asexual plant having the diploid number, meiosis taking place at the first division of the spore mother-cells. This corresponds with what is found in the higher plants, but the two plants in *Dictyota* bear a close external resemblance to each other.

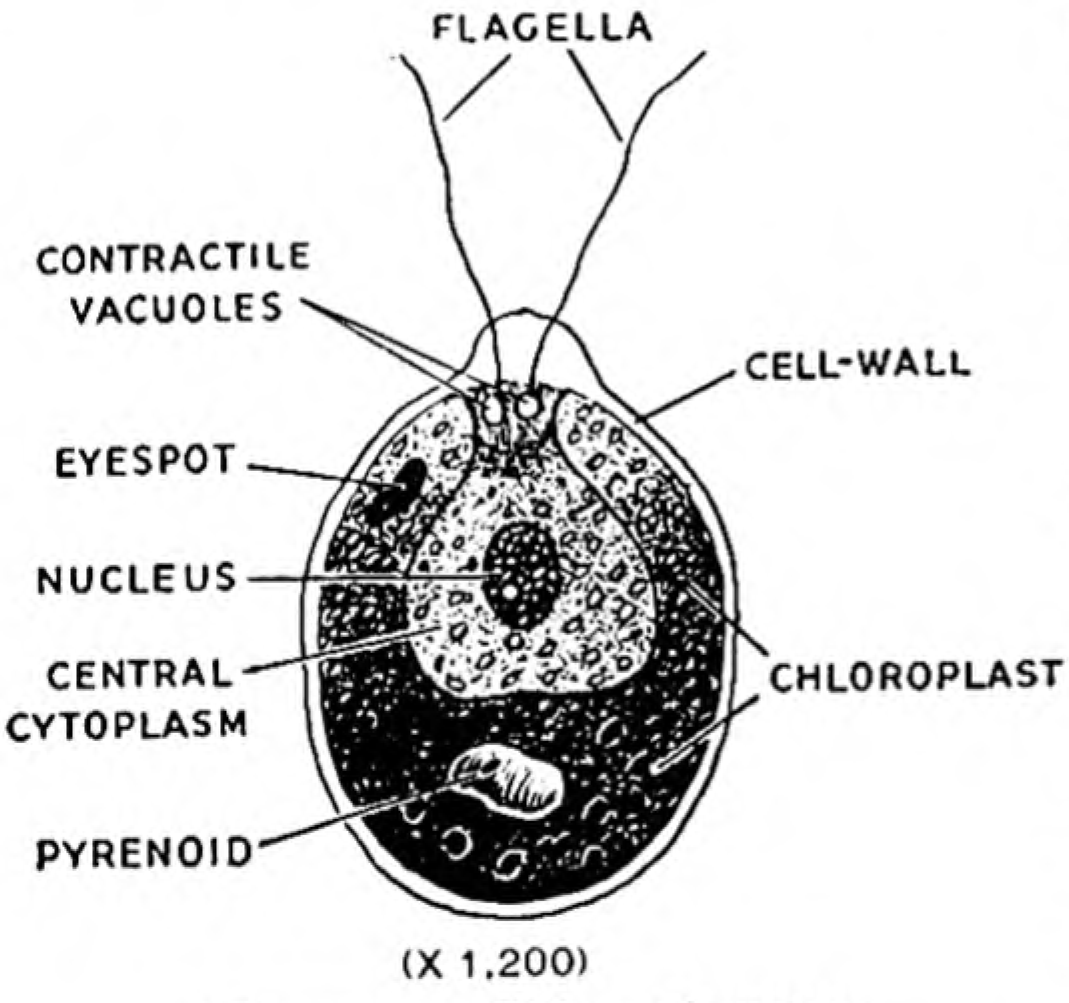

Fig. 357. *Chlamydomonas*.
A motile cell in optical section.

CHLAMYDOMONAS

6. Chlamydomonas

This is one of the unicellular Green Algae. There are about 20 British species, found chiefly in ponds and ditches. There are two phases in the life history—the motile vegetative stage, and the *palmella*-stage. The general structure of the cell is very constant throughout the genus, but the different species present considerable differences in appearance and mode of life.

7. Structure of the Cell (Fig. 357)

The motile cell is usually more or less spherical or ovoid in shape. It has a cellulose wall which is in close contact with the protoplasmic contents. The protoplasm at the anterior region gives off two **flagella** or **cilia** which pass through the cell-wall. The protoplasm in this region also has two **contractile vacuoles** (*i.e.* spaces, filled with liquid, which show alternate expansion and contraction), situated at the base of the cilia, and an orange-coloured **pigment-spot** or **eye-spot** placed laterally. Posteriorly the protoplasm contains a single, large, more or less cup-shaped **chloroplast**, in which is embedded a rounded body known as the **pyrenoid.** The presence in the cell of a small number of large chloroplasts tends to be a characteristic of the Algae and contrasts with the condition in higher plants where generally the chlorophyll-containing cells have a large number of small chloroplasts. A single **nucleus** is present in the central region of the protoplasm enclosed within the cavity of the chloroplast.

The cells move through the water by means of their cilia. The movement is automatic, but is often directed by external stimuli (e.g. light). The cells move towards bright diffuse light and away from light of too great intensity. This sensitiveness to light is specially associated with the eye-spot.

The pyrenoid consists of protein substances. Its function is not known with certainty, but it may represent a store of food-material. From the fact that it is frequently surrounded by small starch grains it has been suggested that it may play a part in the process of photosynthesis. Pyrenoids are frequently associated with the chloroplasts of Algae.

The function of the contractile vacuoles is not understood, but they may be respiratory organs, or perhaps excretory organs, or both. In a few species of *Chlamydomonas* (e.g. *C. nivalis*) the cells sometimes develop a considerable quantity of red pigment (haematochrome), lose their cilia and pass into a resting state known as encystment. The blood-red patches sometimes found in snow in various regions are due to such cells.

Growth consists entirely of cell enlargement, and when the cell has reached a certain size the cell expansion is usually followed by cell-division (asexual reproduction). The nutritional processes are essentially like those of other green plants.

8. Asexual Reproduction (Fig. 358, A, B)

When this is about to take place the cells withdraw or cast off their cilia, and come to rest. The contents of the cells by repeated division give rise to 4, 8 or 16 protoplasts which develop two cilia each, and form **zoospores.** These, usually forming a cell-wall while still enclosed in the mother-cell, produce the motile stage again. They are liberated by decay of the wall of the mother-cell, when they grow and later themselves reproduce.

9. Palmella Stage

In certain undetermined circumstances the daughter-cells which normally form zoospores do not develop cilia. The wall of the mother-cell becomes gelatinous or mucilaginous. Then the daughter-cells undergo division and *their* walls become gelatinous, and so the process goes on until a gelatinous mass is produced, with numerous cells embedded in it. This is known as the **Palmella stage.** In *Chlamydomonas* the *Palmella* stage is usually of short duration. After a time the cells develop cilia, escape from the mucilage and produce the motile stage again. Sometimes the cells of the *Palmella* stage form thick-walled resting spores (hypnospores), whose contents may be coloured red. The red hypnospores of *Chlamydomonas nivalis* are responsible for " red snow."

10. Sexual Reproduction (Fig. 358, c, d)

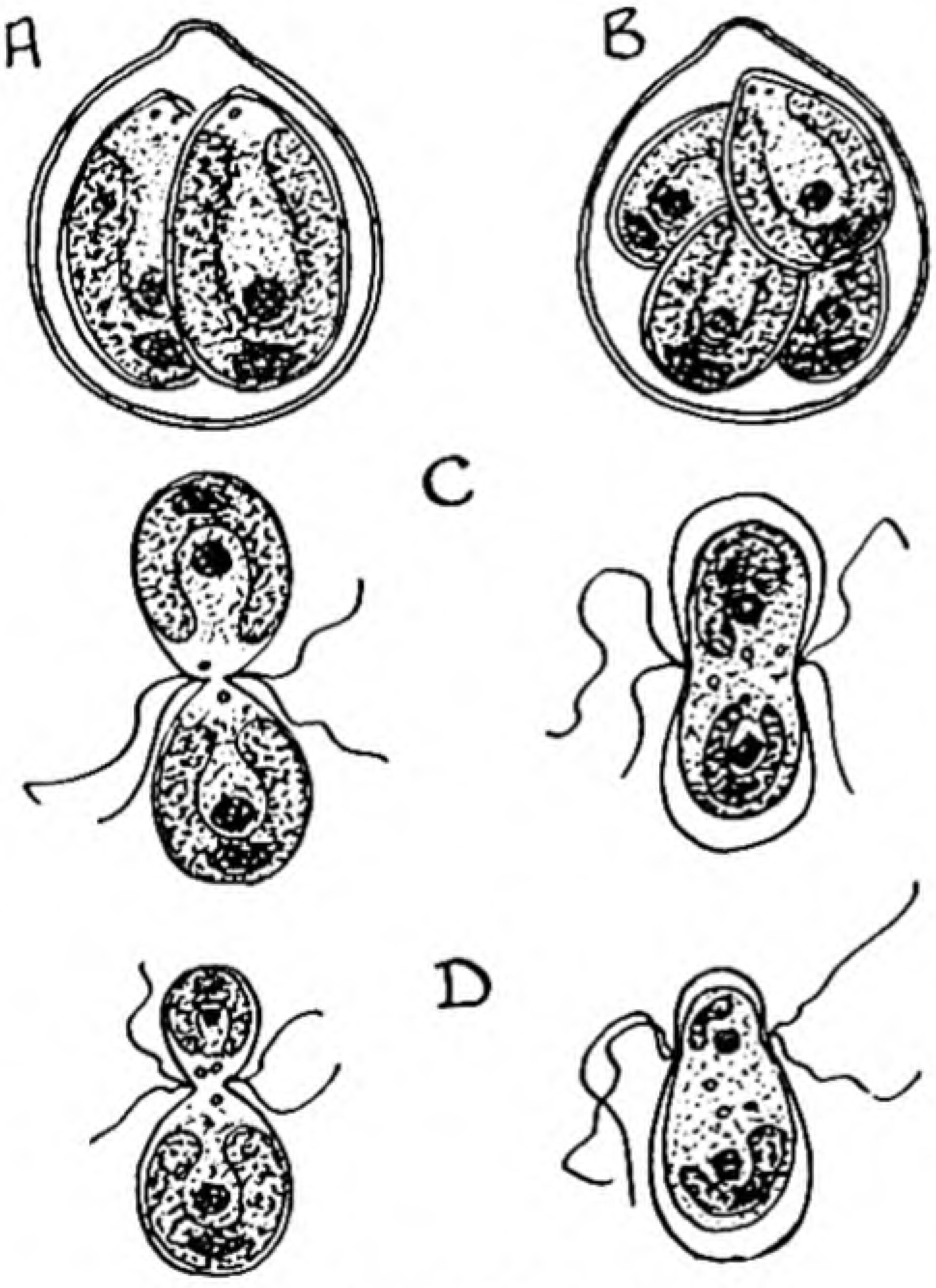

Fig. 358. *Chlamydomonas.*
A, B, Asexual reproduction;
C, D, Sexual reproduction;
C, Isogamous, D, Anisogamous.

The contents of ordinary cells divide into 16, 32 or 64 parts. These are liberated as small, usually naked gametes which otherwise resemble the zoospores. The gametes are more or less pear-shaped and have two cilia. They unite in pairs, usually from different parents, by their ciliate ends and fusion of their protoplasm and nuclei then takes place. The cilia are withdrawn and a thick cell-wall is formed. The zygospore thus formed contains oil and a red or orange pigment. After a period of rest the zygospore gives rise to two or four zoospores by division of its contents. Meiosis probably accompanies this division. The zoospores produce the motile vegetative stage.

In some species the gametes are provided with cell-walls, and in fusing the contents of one gamete pass into the other. In other species whose gametes possess membranes the latter may be discarded before fusion.

Then again, marked anisogamy may occur as in *C. Braunii.* Here large macrogametes withdraw their cilia and come to rest. A small microgamete becomes attached to the macrogamete, their membranes coalesce to form a common envelope within which the two nuclei and protoplasts unite. The resulting protoplast secretes its own cell-wall.

11. *Chlamydomonas* is interesting because it is believed to be, in many respects, a primitive type. It shows affinities with the Flagellata, a group of organisms, which exhibit both plant and animal characteristics. Some of them are holophytic, *i.e.* they possess chlorophyll and are able to elaborate their food-material from simple inorganic compounds. Others feed on organic compounds. Both animal and vegetable kingdoms are believed to have taken their origin from types resembling the Flagellata, and *Chlamydomonas* is supposed to approximate closely to the ancestral organisms from which the vegetable kingdom has been derived. The *Palmella* stage of *Chlamydomonas*, accompanied by cell-division, may be regarded as the starting point of the vegetative stage of higher types; the motile vegetative condition of *Chlamydomonas* is in higher types represented only by the reproductive cells.

SPHAERELLA

12. Sphaerella

In structure, life history, and mode of life *Sphaerella* (Fig. 359) closely resembles *Chlamydomonas*. The two genera belong to the same family of Algae. The following are the more important differences:—In *Sphaerella* the firm outer layer of the cell-wall is separated from the protoplasmic contents by a thick transparent mucilaginous layer which is traversed by protoplasmic filaments; there are numerous contractile vacuoles; the chloroplast is a reticulate body situated at the periphery of the protoplast, and it contains several pyrenoids.

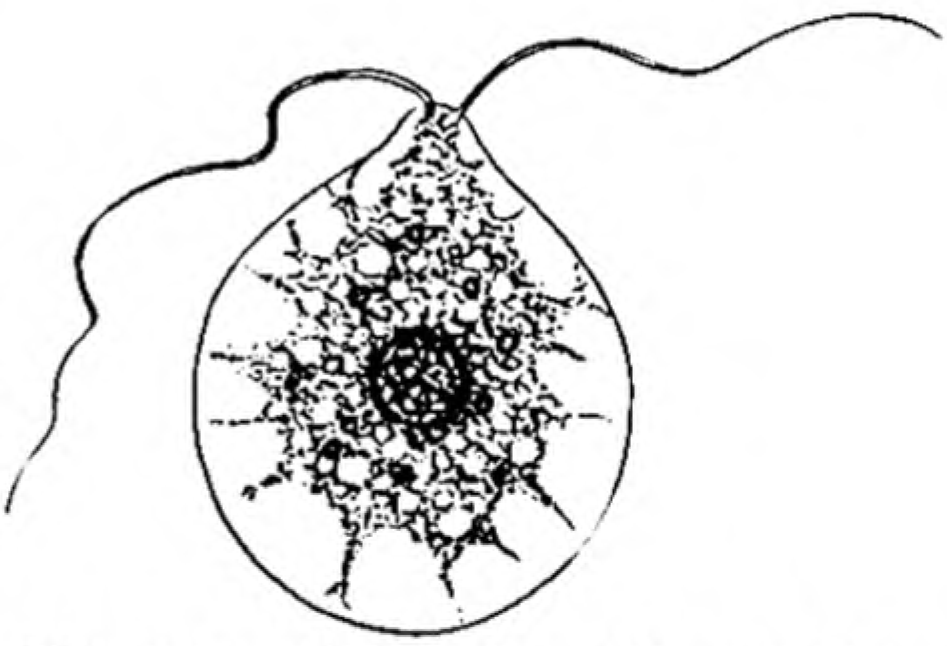
Fig. 359. *Sphaerella*. MOTILE CELL.

Sphaerella lacustris (*Haematococcus pluvialis*) is a common species. Its cells, both resting and motile, like those of other species, often contain much haematochrome and the phenomenon of " red rain " is sometimes due to it. The resting cells are frequently found in rain water which has collected in the hollows of rocks, in gutters, or in water-butts. In *Sphaerella* the gametes appear to be the product of resting cells.

PANDORINA, EUDORINA AND VOLVOX

13. These are three colonial Algae, each consisting of a colony of *Chlamydomonas*-like cells embedded near the surface of a sphere of mucilaginous substance. In the largest of them, *Volvox*, there are

many hundreds, or even thousands, of these cells. Such a colony or *coenobium* (Gk. " common-life ") behaves in many ways as a single individual, swimming, for instance, towards the light, all the cells co-operating in the locomotion.

PANDORINA

14. Habitat and Structure

The colonies are to be found in ponds and ditches in the summer. The spherical colony consists of sixteen cells, embedded in a common mucilaginous matrix. Each cell is somewhat conical in shape, with the base of the cone outwards. From the middle of this broad end two cilia run through the mucilaginous investment to the exterior. These cilia propel the whole colony along in such a way that there is a definite anterior end; and in the cells at this end there are red-brown eye-spots, which appear to be light-sensitive.

15. Asexual Reproduction

In asexual reproduction, each of the sixteen cells of the coenobium divides four times, producing sixteen zoospores, surrounded as a group by their own mass of mucilage, and these groups are then liberated into the water by the softening and disintegration of the mucilage of the parent coenobium (Fig. 360, B and C). Each group now grows into an adult coenobium.

16. Sexual Reproduction

In this process, each cell of a coenobium divides into sixteen or thirty-two parts which become gametes. *Pandorina* is essentially isogamous. It has been claimed that the gametes produced by an individual coenobium will not fuse in pairs, but only those of different coenobia. If this is true the coenobia must be regarded as showing a physiological differentiation of sex. Also in *Pandorina* there is a trend towards anisogamy in that some coenobia produce smaller and others larger gametes, and a microgamete fuses with a macrogamete.

The zygote resulting from fusion of protoplasts and nuclei becomes invested in a thick, smooth cell-wall. Oil is stored as reserve food-material and an orange or red colour develops, probably due to haematochrome. The zygote is capable of surviving a long period of rest. On germinating it is probable, by comparison with allied forms, that meiosis occurs. Of the four cells resulting from the division of the zygote, only one develops. This escapes as a single zoospore from the zygote membrane, and soon divides to give rise to a coenobium.

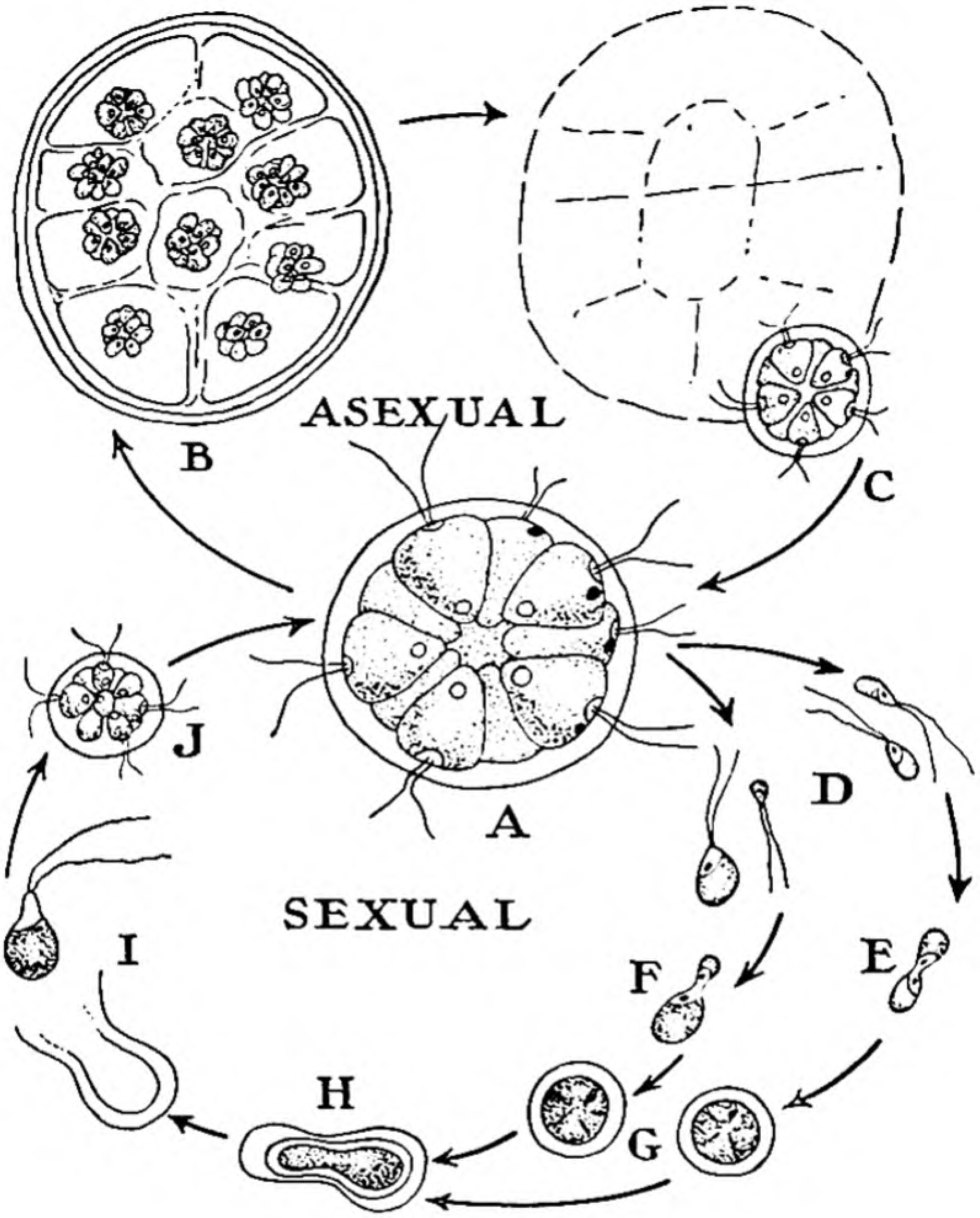

Fig. 360. *Pandorina.*

A, Parent colony; B, each cell of A dividing to form a daughter-colony; C, Daughter-colony escaping from parent matrix, and soon growing into the form at A; D, Gametes; E, Isogamy; F, Anisogamy; G, Zygospores; H, a zygospore germinating; I, Zoospore liberated from H; J, New colony forming by division of I.

EUDORINA

17. Habitat and Structure

The habitat is the same as in *Pandorina*. The coenobium is larger than in *Pandorina*, and consists of thirty-two more or less spherical cells, not packed so tightly together as in *Pandorina*, but lying at intervals near the surface of a hollow mucilaginous sphere.

As in *Pandorina*, all the cells are alike, except that the pigmented "eye-spots" are very much better developed at the "anterior" end of the colony than they are at the opposite end. Unlike *Pandorina*, however, the cells are connected together by very fine protoplasmic threads.

18. Asexual Reproduction

This method is very similar to that in *Pandorina* except that each cell of the parent colony divides up to form its own little colony of thirty-two cells instead of sixteen.

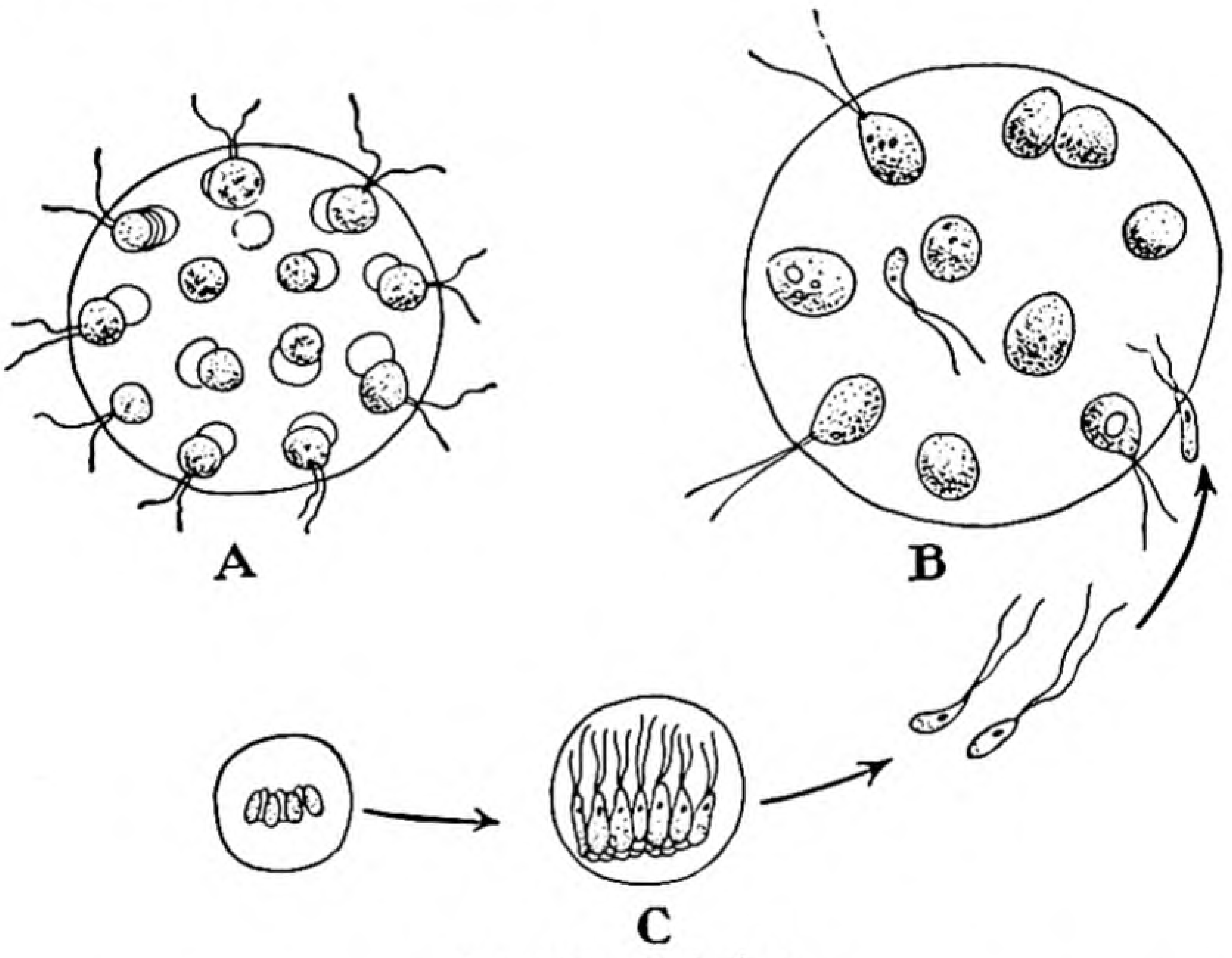

Fig. 361. *Eudorina.*

A, Adult colony; B, Female colony, with egg-cells awaiting spermatozoids; C, Three stages in the formation of the spermatozoids.

19. Sexual Reproduction

This is more advanced than in *Pandorina* in a number of ways. In the first place, the colonies are dioecious, and the gametes highly differentiated.

The female gametes, or egg-cells, arise from what are apparently ordinary vegetative cells of the colony, except that they are somewhat larger than the rest, and soon lose their cilia. They appear to reach the surface of the mucilaginous matrix, but never actually leave it (see Fig. 361, B).

The male gametes, or spermatozoids, are formed by successive divisions of each cell of a "male" colony, giving "plates" of male cells. Each " plate " generally leaves the parent colony as a group of sixty-four cells, which swims as a unit to a female egg-cell and then breaks up into individual spermatozoids. These fuse with egg-cells forming smooth-walled zygotes or " oospores," which germinate to produce a new colony.

The spermatozoid is long and narrow in shape, and has no green chloroplast, the only colour present being a slight yellow tint at the end furthest from the cilia.

Often in *Eudorina* some of the cells at the anterior end of the colony are purely vegetative and take no part in the reproductive processes.

VOLVOX

20. Habitat and Structure

Volvox may often be found as minute green balls, just visible to the naked eye, swimming in fresh-water ponds. Multiplication is sometimes so rapid in summer that the water of small ponds may be coloured green by it.

Volvox is the largest and most highly differentiated of the coenobial forms. The colony consists of some hundreds or thousands of cells embedded near the surface of a sphere of mucilage which is very soft at the centre, but firmer at the surface. The cells are connected together by protoplasmic strands, forming a fine, continuous, spherical network (see Fig. 362, A). Each cell has a green chloroplast, usually oval, a reddish-brown eye-spot, one or more pyrenoids, contractile vacuoles, and two cilia (seen more clearly on staining with iodine), which project beyond the surface of the colony.

21. Asexual Reproduction

During the summer reproduction proceeds rapidly by an asexual method, through generation after generation. The great bulk of the cells in the colony are purely somatic; *i.e.* they can not reproduce. If, however, we study some young coenobia, we may observe a few large round cells, with a well-defined nucleus and dense, granular protoplasm situated in the posterior region of the coenobium. These are the " parthenogonidia "—cells specialised for non-sexual reproduction (see Fig. 362, B).

Each of these parthenogonidia, of which seldom more than a dozen are found in any one colony, proceeds to divide, forming a group of two, four, then eight cells, and finally a multicellular plate, curving inwards at the middle like a saucer, towards the centre of the colony. After a time this plate inverts, thus bringing to the

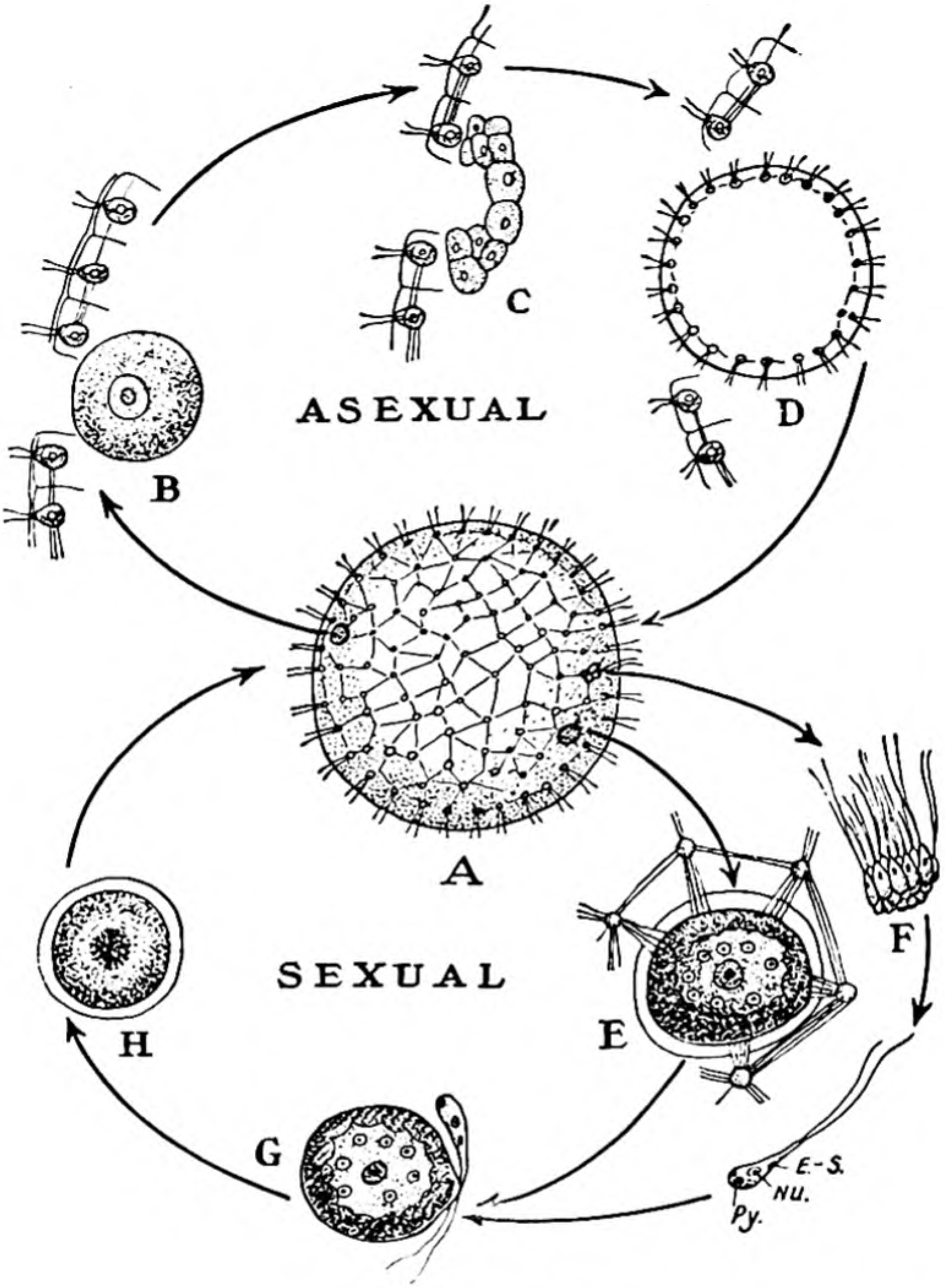

Fig. 362. *Volvox.*

A, Parent colony; B, Parthenogonidium in sectional view; C, Early stage in division of parthenogonidium to form a new daughter-colony; D, Daughter-colony breaking through surface of dying parent-colony; E, Egg-cell in surface view; F, Spermatozoids; G, Fertilisation; H, Oospore; A × 150; all others × 850.

outside of the new colony the ends of the cells at which the flagella will develop; while at the same time the cells, which up till now have been in contact, begin to separate from one another by the development of the mucilaginous cell-walls. In this way a new daughter-colony is formed inside the parent-colony, at whose death and disintegration the daughter-colonies are liberated to the exterior (see Fig. 362, C, D).

22. Sexual Reproduction

In the autumn, often in the same coenobium as the parthenogonidia, there may be found sexual reproductive cells. Some cells are large and round, and connected to a number of the surrounding vegetative cells by fine protoplasmic threads. They develop into female gametes, or egg-cells, with no cilia, a large central nucleus, and a peripheral chloroplast containing numerous pyrenoids, giving the whole cell a very granular appearance. They often develop a prominence called a " beak." Other cells divide to form a plate or disc of male cells or spermatozoids, as in *Eudorina*, whose spermatozoids they resemble in their long, narrow shape, biciliate condition, yellowish coloration, and large nucleus relative to size of the cell (see Fig. 362, E, F).

On fertilisation a spherical resting-spore or oospore with a thick wall and red or brown colour is produced. It germinates, and by repeated cell-division produces a new coenobium (see Fig. 362, G, H).

23. The preceding three colonial forms together with *Chlamydomonas* suggest a possible line of evolution of a thallus. First of all an aggregation of similar cells as in *Pandorina*. Here, although the colony behaves as a single unit, its cells are almost independent.

In *Eudorina*, the cells of the colony are connected by protoplasmic strands, so that there is a definite plant body, but still each cell is capable of carrying on all the processes of nutrition, and in some species the processes of reproduction. In some species of *Eudorina* specialisation has developed, only the cells at one end of the colony being concerned with reproduction. The development of specialised reproductive cells is more marked in *Volvox* which shows also a great increase in the size of the colony. This particular type of body organisation appears to reach its culmination in *Volvox*. Concurrently with increased specialisation of body structure is an increasing specialisation of reproduction. For example, the anisogamous sexual reproduction of *Pandorina* gives place to the well-developed oogamy of *Volvox*.

PLEUROCOCCUS NAEGELII

24. Pleurococcus

This is one of the commonest terrestrial Green Algae, forming the green covering so frequently seen on tree-trunks, palings, etc. The cells of *Pleurococcus* can withstand considerable desiccation without being damaged, indicative perhaps of special protoplasmic properties which enable loss of water from the cell to take place without any accompanying irreversible change taking place in the protoplast itself. The Alga was formerly known as *Protococcus viridis*.

25. Structure of the Cell (Fig. 1)

If a little of the green substance is examined in water under the microscope it is found to consist of small green cells, sometimes single, sometimes aggregated into groups or colonies of two, four, or more. The individual cells are almost spherical if isolated, but in the cell-groups they are slightly flattened on the sides in contact with the other cells.

Each cell has a firm cellulose wall. Embedded in the protoplasm on one side is a single, large, lobed **chloroplast.** A **nucleus** is present in the centre of the cell. There are no pyrenoids.

26. Reproduction

The only method of multiplication known with certainty is by cell-division and separation of the daughter-cells from each other. In very moist conditions the cells may not separate, and in this way small colonies of cells may be formed.

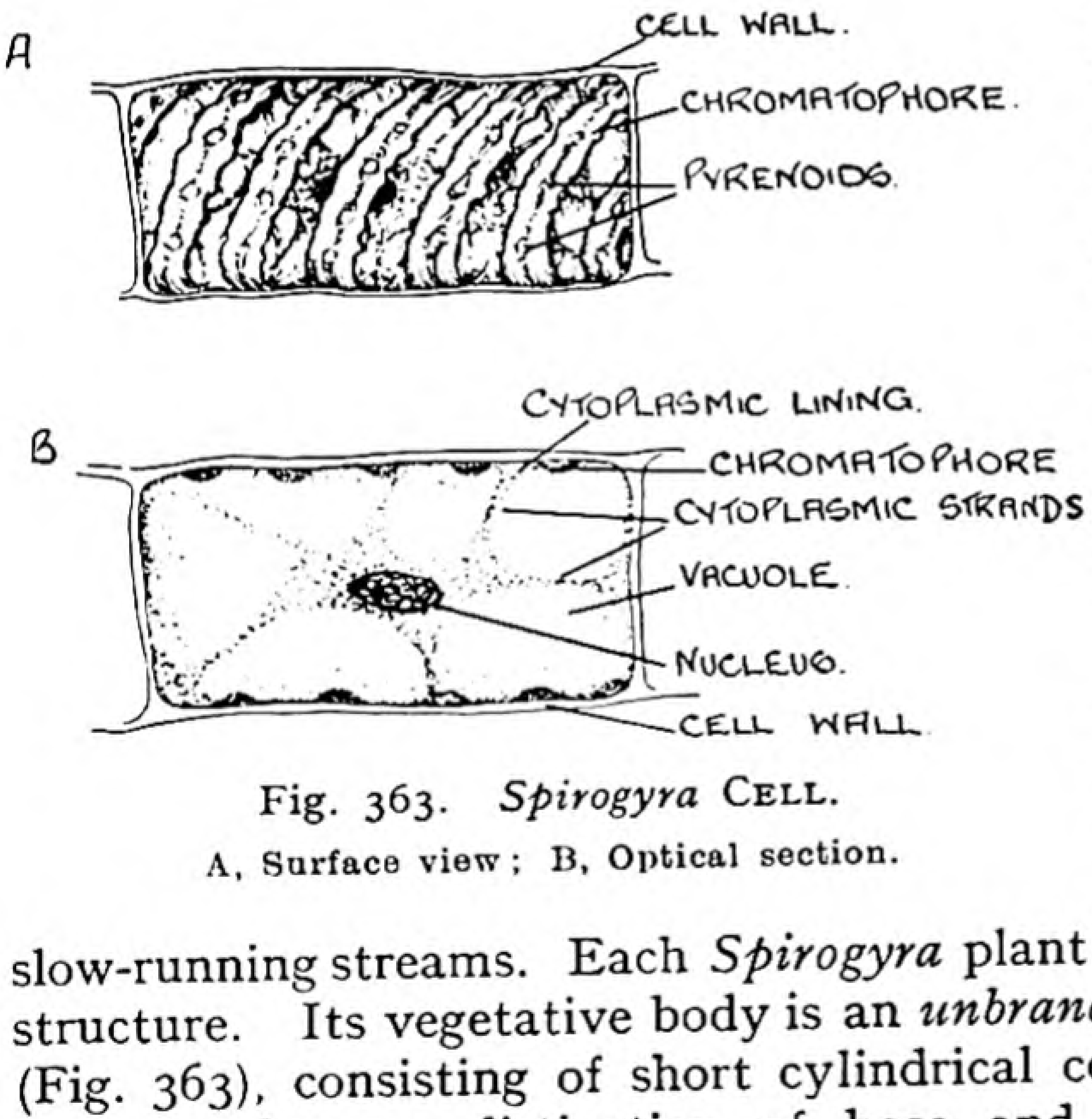

Fig. 363. *Spirogyra* CELL.
A, Surface view; B, Optical section.

SPIROGYRA

27. General Characters

Spirogyra is one of the freshwater Green Algae. It forms bright-green slimy masses in ponds, and slow-running streams. Each *Spirogyra* plant has a relatively simple structure. Its vegetative body is an *unbranched* filamentous **thallus** (Fig. 363), consisting of short cylindrical cells placed end to end and showing no distinction of base and apex. The filament increases in length by cell-division and growth of the cells. All the cells have the same structure and all are capable of division.

Here we have an example of a multicellular plant which shows little or no division of labour. Indeed, each cell might be regarded as an individual plant, and the whole filament as a colony of such individuals, for each cell carries on all the vital functions necessary for its continued existence.

The filament is, in most species, invested by a delicate mucilaginous sheath formed by the cell-walls. It is this which makes a mass of Spirogyra filaments feel slimy to the touch.

28. Structure of the Cell (Fig. 363)

Each cell is cylindrical in form with transverse end-walls, and has the structure characteristic of parenchymatous cells. The wall consists of cellulose and pectic compounds. Inside the cell-wall there is a lining of cytoplasm, from which delicate **protoplasmic strands** run across a central **vacuole** to the centre of the cell. The **nucleus**, containing a nucleolus, is usually embedded in the small central mass of cytoplasm. The most conspicuous structures in the cell are the green spirally-coiled **chromatophores** (chloroplasts). There may be from one to seven of them in a cell, the number varying slightly even in the same species. They lie in the cytoplasm and each contains a number of well-marked **pyrenoids**.

In cell-division the transverse wall separating the two daughter-cells is formed by annular ingrowth from the longitudinal wall of the mother-cell (Fig. 364, A). In some of the smaller species of *Spirogyra* the transverse wall does not remain plane and single, but splits in the middle into two circular discs, which may be shaped like a biconvex lens. The cavity is probably filled with mucilage. In other species there is a peculiar ingrowth of the developing cell-wall on either side to form a circular ridge. This is known as the replicate condition.

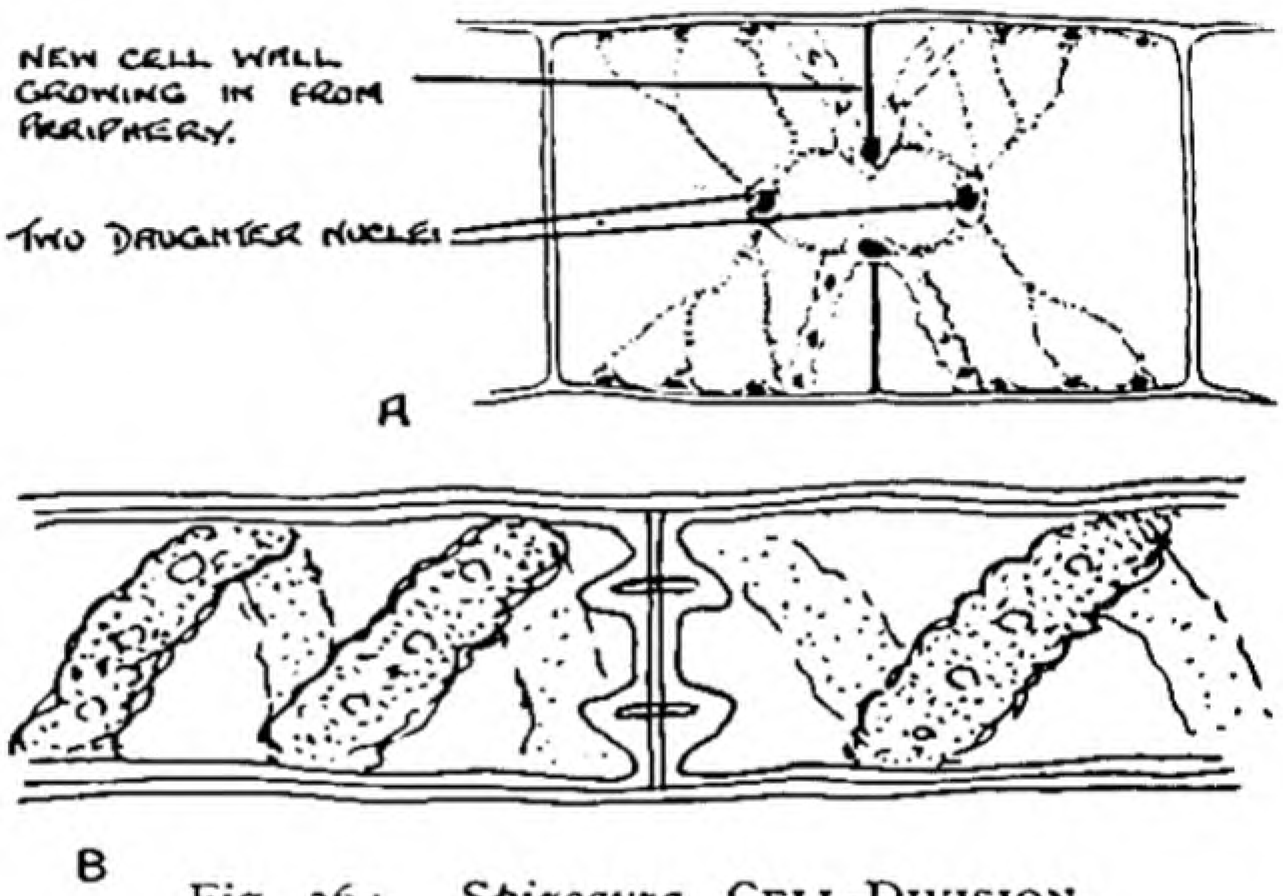

Fig. 364. *Spirogyra*, CELL-DIVISION.
A, Early stage; B, Replicate condition.

The numerous species of *Spirogyra* are distinguished according to the character of the transverse walls, the number of chloroplasts per cell, the number of spiral turns in one chloroplast, the characters of the cells containing the zygospores and of the zygospores themselves.

29. Reproduction

There is no special method of asexual reproduction; but filaments may break into a number of pieces, consisting of one or several cells, and these by ordinary cell-division may form new filaments (vegetative reproduction). Fragmentation of this kind may occur naturally, and results in a rapid multiplication of *Spirogyra* when conditions are favourable.

Sexual reproduction (Fig. 365) is isogamous, and, in north temperate regions, generally occurs from about February to June. The process is termed conjugation, and whilst it usually takes place between two filaments, more than two may be involved in it. Movements, the causes of which are unknown, bring the filaments into such close contact that they coalesce. Along the line of contact slight protrusions arise from the cells of one of the two filaments and are followed by corresponding and opposite protrusions from the cells of the other filament. As these protrusions elongate, the two filaments are gradually pushed apart, and the conjugation tubes are formed. When they have reached full growth their end-walls disappear and the protoplasts are now in direct contact. In the early stages of the conjugation process starch accumulates in the cells concerned, and the protoplasts of the cells of one filament begin to show plasmolysis effects some time before those of the other side. For this reason, and because of subsequent behaviour, the filaments are distinguished as male and female respectively. The male protoplast as it contracts remains in contact with the female, and passes over into the female cell through the conjugation tube. It is only at this stage that the female protoplast contracts. The chloroplasts of the male protoplast usually disintegrate at an early stage, and the fusion of the nuclei may be delayed. The starch is converted into fat, which is often

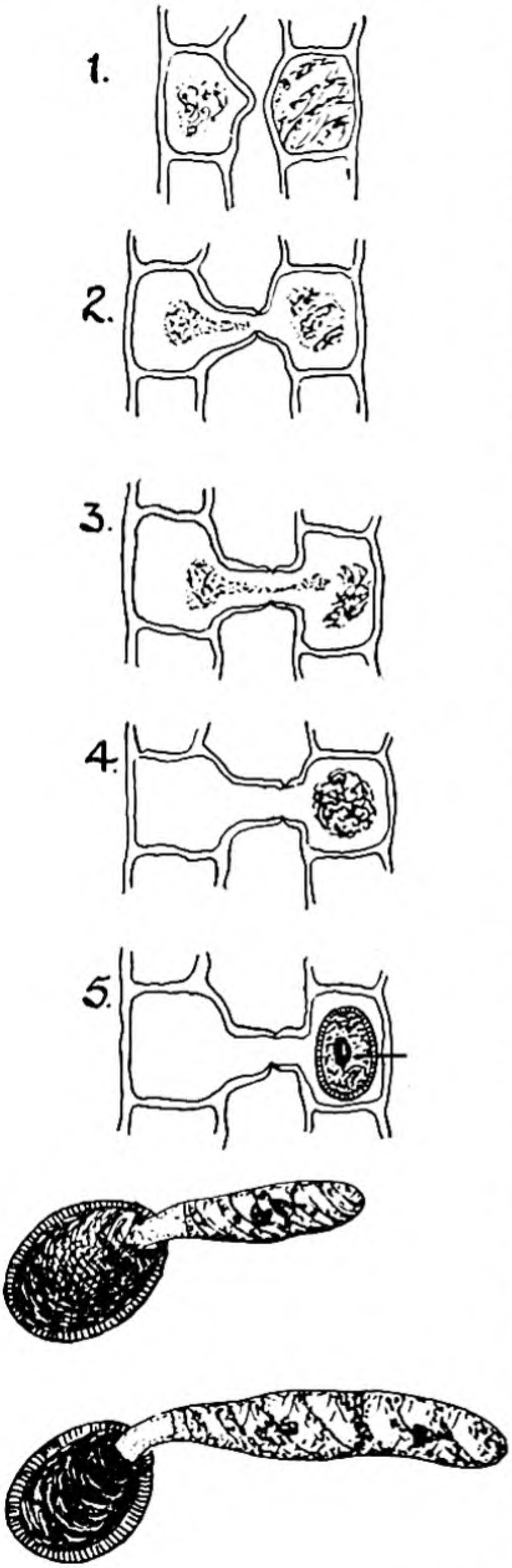

Fig. 365. *Spirogyra*. Stages in Conjugation and Germination of Zygospore.

coloured red. A thick resistant wall is secreted, and the ripe **zygospore** thus formed may be spherical or ellipsoidal in shape. The zygospores are liberated by the decay of the cell-wall of the female filament and are capable of surviving a period of rest in the substratum even though there may be a seasonal drying of the pond or stream.

The method of conjugation described above is known as ladder-like or **scalariform** conjugation. But in some species of *Spirogyra* conjugation may take place between cells of the same filament. This is known as chain conjugation. Here a joint protrusion appears at a point on the periphery of a filament where two cells are contiguous, the separating wall in this protrusion breaks down and the protoplast of one cell moves across into the other cell where fusion takes place and a zygospore is formed. Such a filament frequently shows two cells containing zygospores alternating with two empty cells along its length.

The protoplasts of conjugating cells may be regarded as gametes, and any cell of a filament may function as a gametangium. The more active gametes are regarded as male, and the more passive ones as female.

In scalariform conjugation, all the cells of a filament are usually either male or female, and the filaments unisexual. It is an extremely rare occurrence for some cells of a filament to act as male and others of the same filament as female. In the genus, *Zygnema*, closely allied to *Spirogyra*, there are species in which the gametes meet, fuse and form zygospores in the conjugation tube. Here the gametes are all alike and conjugation is isogamous.

30. Germination of the Zygospore

The result of conjugation is the formation of a zygospore (Fig. 365). The division of the diploid nucleus may take place soon after fusion, or during the maturation of the zygospore, or immediately before germination. There are usually two successive nuclear divisions, associated with meiosis. One of the four resulting haploid nuclei enlarges, the other three gradually abort. Preparatory to germination the stored fat is converted into starch and the chloroplasts become more readily discernible. At one end of the zygospore a germ tube protrudes through the ruptured outer layers of the thick cell-wall. This becomes divided into two cells by a transverse septum. The lower cell has little chlorophyll and may be almost colourless. In some species there is a tendency towards a rhizoid-like development, but the zygospore membrane more or less envelops it for a time. The upper cell divides further to form the *Spirogyra* filament.

31. *Spirogyra* belongs to a group of the Chlorophyceae known as the Conjugales.

ULOTHRIX

32. Habitat and Structure

Ulothrix is a common filamentous green Alga, found as a green mass floating on rivers and streams or attached to stones. The filaments are slender and unbranched and consist of short cells, each a little wider than it is long. Each cell contains a single band-like chloroplast possessing pyrenoids and embedded in the cytoplasm that forms a lining to the cellulose cell-wall. A single nucleus is found in the cytoplasm of each cell. The basal cell of a filament may form a colourless unbranched attaching organ (Fig. 366, A). Apart from the chloroplast, there is thus a superficial resemblance between *Ulothrix* and *Spirogyra*. There are striking differences, however, in the reproduction of these two Algae.

33. Vegetative Reproduction

Especially during cool weather the filaments increase in length by cell division and then break up into fragments. Each portion of filament then grows as before and forms a new filament. This method of fragmentation permits rapid vegetative increase when conditions are suitable for growth.

34. Asexual Reproduction

Ulothrix reproduces asexually by means of "swarmspores" or zoospores. This generally occurs in the cool season, and the contents of some or all of the cells of the filament divide into two, four or eight nucleated portions which are set free through a lateral opening which develops on the cell-wall, as free-swimming, naked (*i.e.* devoid of a cell-wall), pear-shaped zoospores. Occasionally the contents of a cell of the filament give rise to a single zoospore only. Each zoospore has four cila at its pointed anterior end, a single chloroplast with a pyrenoid near the posterior end, a red pigment-spot and two contractile vacuoles (Fig. 367, A). After swimming for a period of a few hours, the zoospore settles and attaches itself by the ciliated end to some submerged surface. The cilia are withdrawn, a cell-wall develops and by cell division a new filament arises. In addition to the large four-ciliated zoospores, smaller biciliated ones may be produced.

Occasionally the cells of a filament divide into a number of rounded green bodies which secrete mucilage in which they remain embedded (Fig. 366, B). This resembles the *Palmella* stage of *Chlamydomonas*. Later the cells may be liberated as zoospores and give rise to new filaments. During periods of drought the contents of the cells of the filament may round off and secrete thick walls so that a chain of resting spores is produced (Fig. 366, C). These become separated from each other. Later, in water, each spore gives rise to a new filament.

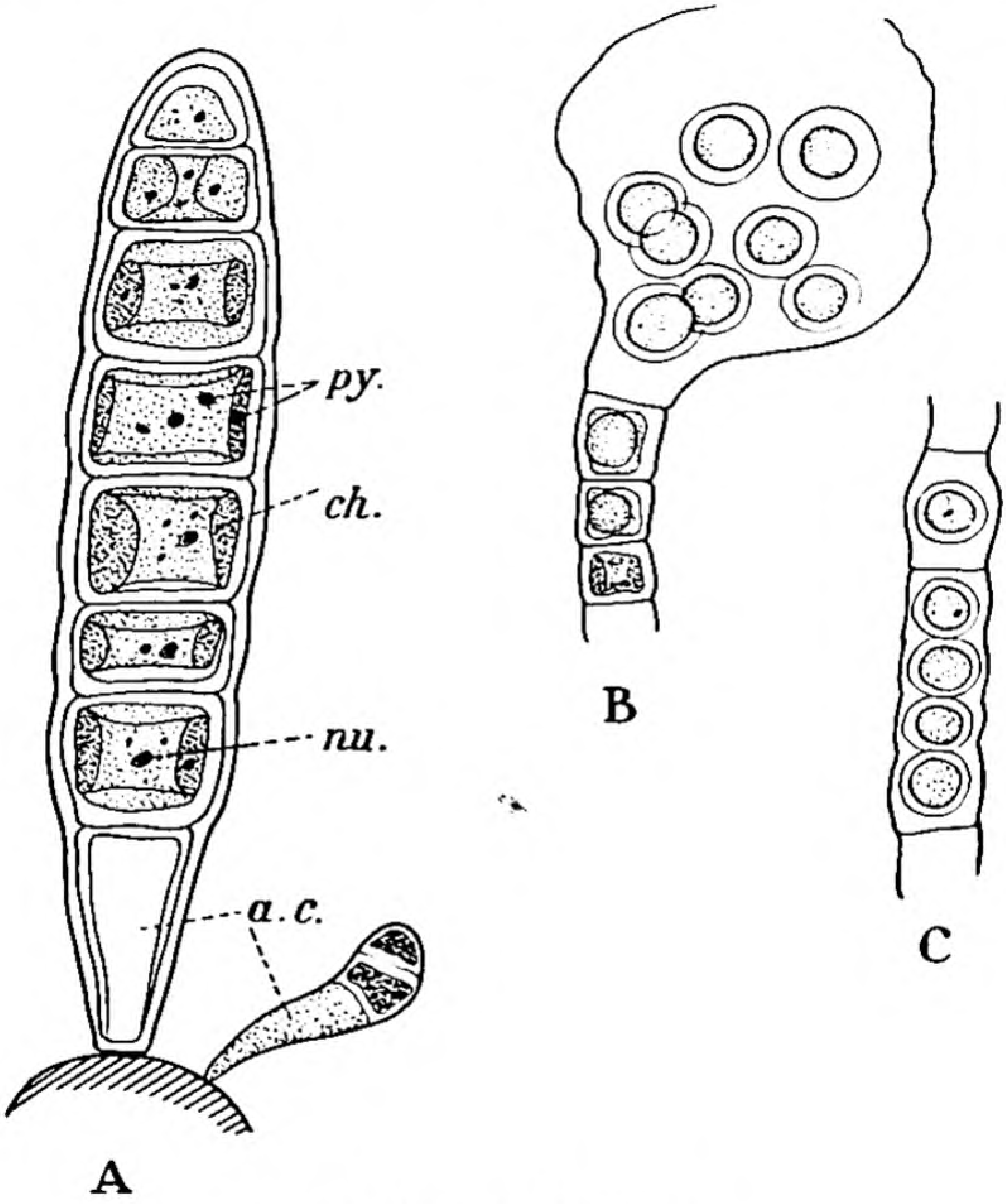

Fig. 366. *Ulothrix zonata.*

A, Young filaments, growing attached to a stone; *a.c.*, attaching cell, *nu.*, nucleus, *ch.*, chloroplast, *py.*, pyrenoids. The smaller filament has just developed from a swarmer (see Fig. 367, A); B, Palmella condition; C, chain of resting-spores.

35. Sexual Reproduction

Gametes are produced in a manner similar to zoospores, but each cell gives rise usually to sixteen or thirty-two gametes which are all alike (i.e. *Ulothrix* is isogamous), smaller than the zoospores, and biciliate. The gametes are liberated, and after swimming for a while, fuse in pairs to form a motile zygote with four cilia, two eye-spots and two chloroplasts. After a short time the zygote withdraws its cilia, secretes a thick wall and becomes a zygospore. This is a resting spore which can survive periods of drought. Later the zygospore produces a small number of four-ciliated zoospores, each of which may give rise to a new filament (Fig. 367, B-F). The gametes can function as parthenospores, developing directly into new filaments without the intervention of a process of conjugation.

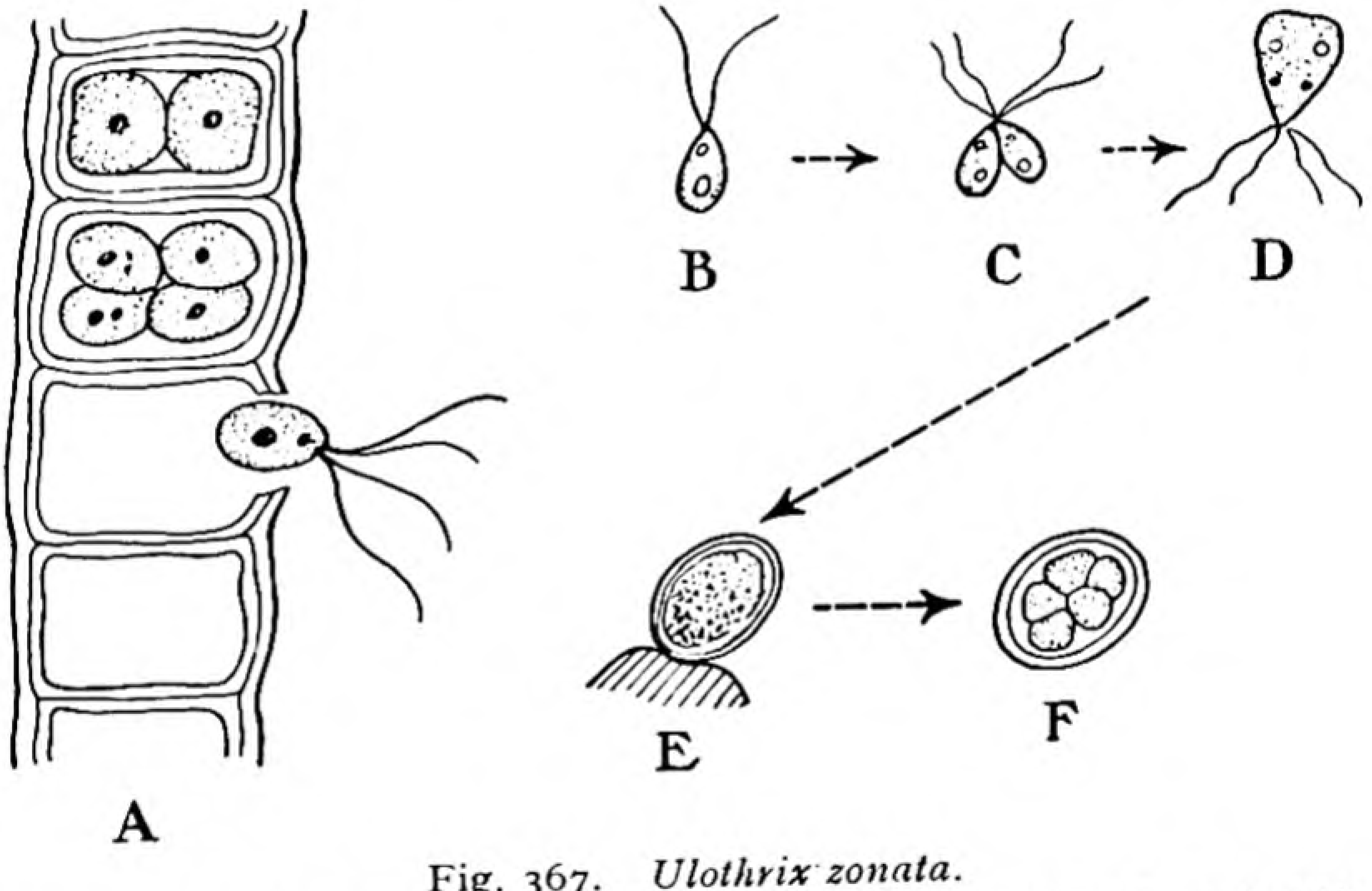

Fig. 367. *Ulothrix zonata.*

A, Formation and liberation of swarmers (asexual); B, gamete; C, conjugation of 2 gametes; D, the resulting zygote, which changes into the zygospore, E; F, germination of zygospore.

VAUCHERIA

36. Structure

Most of the species of this Green Alga grow in fresh water, or on the damp surface of the soil. A few species are marine. *V. sessilis* and *V. terrestris* are commonly found, mixed with other Algae and the protonema of mosses, in the form of a green tangled felt on damp soil.

The thallus (Fig. 368, C) consists of long, rather coarse, branched tubular threads, fixed to the substratum by means of branched colourless rhizoids. The tubes are **non-septate**, *i.e.* they are not divided by cell-walls into distinct cells. Septa, however, are formed when the thallus is injured and in connexion with the development of reproductive organs. The cellulose wall of each tube has a continuous **cytoplasmic lining.** A **vacuole** filled with cell-sap occupies the middle of the tube. In the outer region of the cytoplasm there are numerous discoid **chloroplasts,** and large numbers of small **nuclei** are found in the layer internal to this. There are no pyrenoids. Small refractive **oil-globules** are associated with the plastids. It is interesting to notice that usually no starch is present; here the product of photosynthesis appears to be oil.

Vaucheria was formerly described as a *unicellular* Alga. The branched tubes, however, are not cells, but **coenocytes,** and we have here a good example of coenocytic structure (p. 45). The branches of the coenocyte exhibit apical growth.

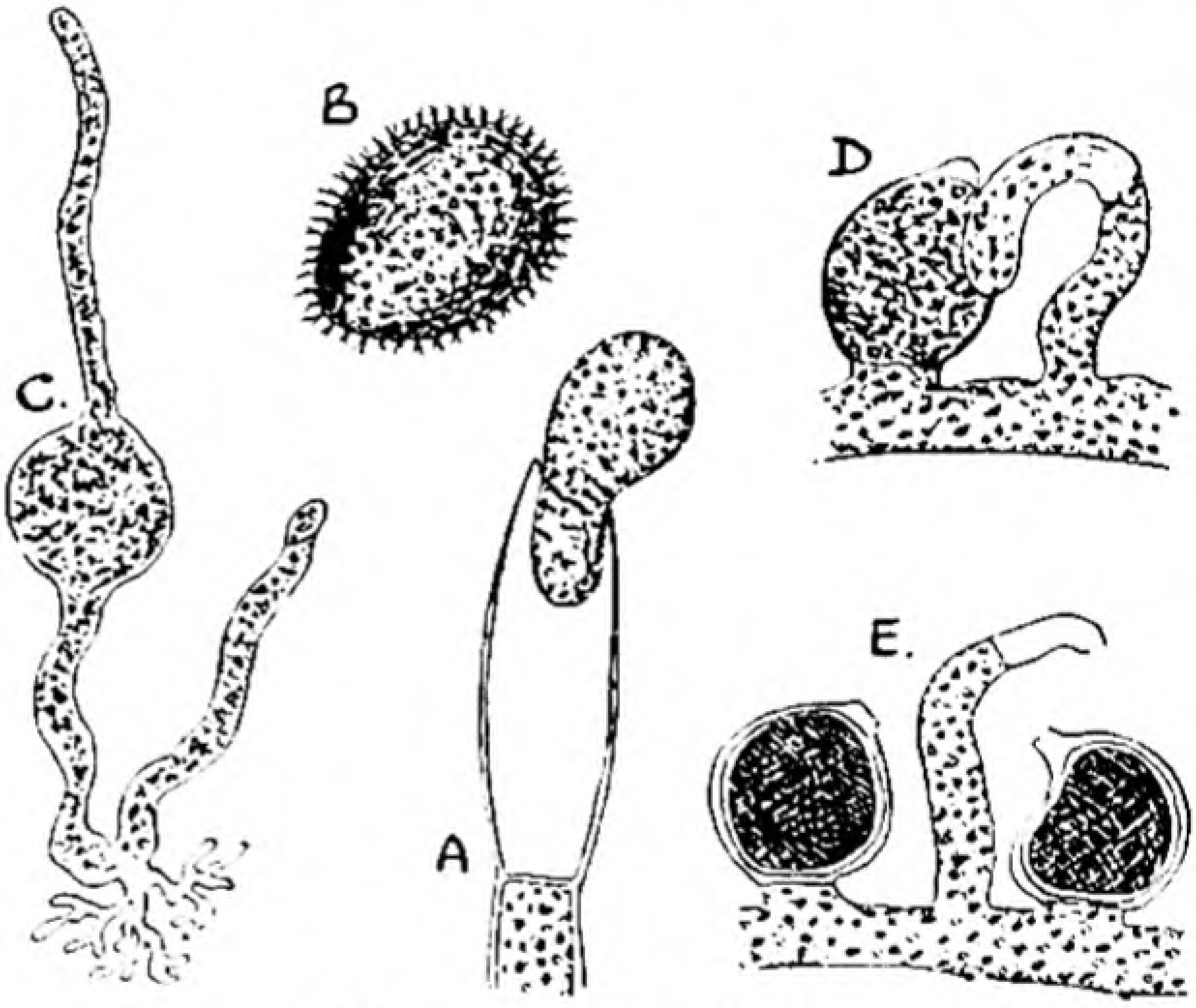

Fig. 368. *Vaucheria.*

A, Zoosporangium liberating zoospore; B, Zoospore; C, Germinated zoospore; D, Antheridium and oogonium; E, Oospores in oogonia, dehisced antheridium.

37. Asexual Reproduction

This is commonly effected by means of zoospores. In the formation of a zoospore the apex of a branch swells up and becomes club-shaped (Fig. 368, A), owing to the aggregation of protoplasmic substance in it. This club-shaped body which is the **sporangium,** is separated from the rest of the tube by a septum. It ruptures at the apex, and the protoplasmic contents escape as a zoospore. The opening is very narrow, and, as the protoplasmic body makes its way out, it is frequently constricted and divided into two often very unequal parts, each of which forms a zoospore.

The **zoospore** (Fig. 368, B) is a large ovoid body which can be seen by the naked eye. It has a superficial hyaline layer of cytoplasm containing the numerous nuclei, beneath which the numerous chloroplasts are embedded. There is a central sap vacuole. The zoospore is covered with **cilia,** a pair being developed opposite to each nucleus. It is probably to be regarded as a compound zoospore, made up of a number of biciliate zoospores which have failed to separate. The multiciliate zoospore, after moving about for a short time (about fifteen minutes) develops a cell-wall and comes to rest. The cilia are withdrawn, and germination takes place. Two tubes grow out. One branches and produces the colourless rhizoid, the other develops into the green tubular thread (Fig. 368, C).

In some species of *Vaucheria* (not *V. sessilis*) in conditions of drought, cilia are not developed. The protoplasmic contents of the sporangium round themselves off, form an investing membrane, and so develop into a non-motile spore (*aplanospore*). This may be liberated by the decay of the wall of the sporangium, or germinate inside the sporangium. Sometimes the contents of the sporangium do not round themselves off, and the sporangium itself may germinate like a spore.

In conditions of drought, the contents of some *Vaucheria* filaments may break up into a number of pieces or segments, which form thick walls and become laden with oil. This is a resting protective condition, and the segments or cysts may remain inside the filament for some time, but on the return of favourable conditions they germinate and produce new plants. This may be considered as a purely vegetative method of reproduction.

38. Sexual Reproduction

Sexual reproduction is heterogamous (Fig. 368, D and E). The male organ is an **antheridium**; the female organ is called the **oogonium.** They arise as outgrowths, either of the tube itself (*V. sessilis*) or of a special short branch, and are usually borne on the same plant. The number of oogonia and antheridia associated together varies in the different species. In *V. sessilis* there is frequently one antheridium between two oogonia (E). A few species are dioecious.

The outgrowth which becomes the antheridium contains numerous chloroplasts and small nuclei. As development proceeds the nuclei aggregate in the central region of the protoplasm and with some of the protoplasm give rise to a large number of very minute biciliate spermatozoids. The chloroplasts pass to the base of the outgrowth, and are cut off by a septum from the portion containing the spermatozoids, which is the antheridium proper. When fully formed the antheridium is a colourless tubular structure curved like a horn (D). It ruptures at the apex, and the spermatozoids are set free.

The outgrowth which forms the oogonium at first contains numerous nuclei in addition to chloroplasts. One nucleus passes to the centre of the protoplasmic mass, and becomes the nucleus of the **oosphere**; the others pass back into the tube. The oogonium is then separated off by a septum. A protuberance or beak appears to one side near the apex. It bursts and a small portion of the protoplasmic contents is extruded. The rest of the contents form the oosphere, which contains numerous chloroplasts. It shows a clear spot—the **receptive spot**—opposite the beak where the protoplasmic vesicle was extruded (D). The fully formed oogonium is sessile, and more or less ovoid in form. It has a simple cellulose wall and contains one oosphere.

Fertilisation is effected by a spermatozoid entering the oosphere at the receptive spot, and fusing with it. The **oospore** develops a thick wall and enters on a period of rest. When it germinates it produces a new plant directly. The first division of the nucleus of the oospore is meiotic.

Vaucheria belongs to a group of Chlorophyceae known as the Siphonales.

Perhaps the most striking feature about *Vaucheria* is the association of highly differentiated sexual organs with an apparently simple vegetative body.

OEDOGONIUM

39. General Characters

Oedogonium is a common Green Alga including numerous species, all living in fresh water. Each plant (Fig. 369, A) consists of an unbranched filament of elongated cells. In the young stages (B, C) the plants are attached to stones or other plants by means of a basal fixing organ (hapteron), but in many species the adult plants are free. The apex of the filament may be rounded, or, in a few species, may end in an elongated hair-like process. The growth of the filament is intercalary and is effected by the division of certain cells known as cap-cells which occur at intervals in the filament. Vegetative reproduction is effected by fragmentation.

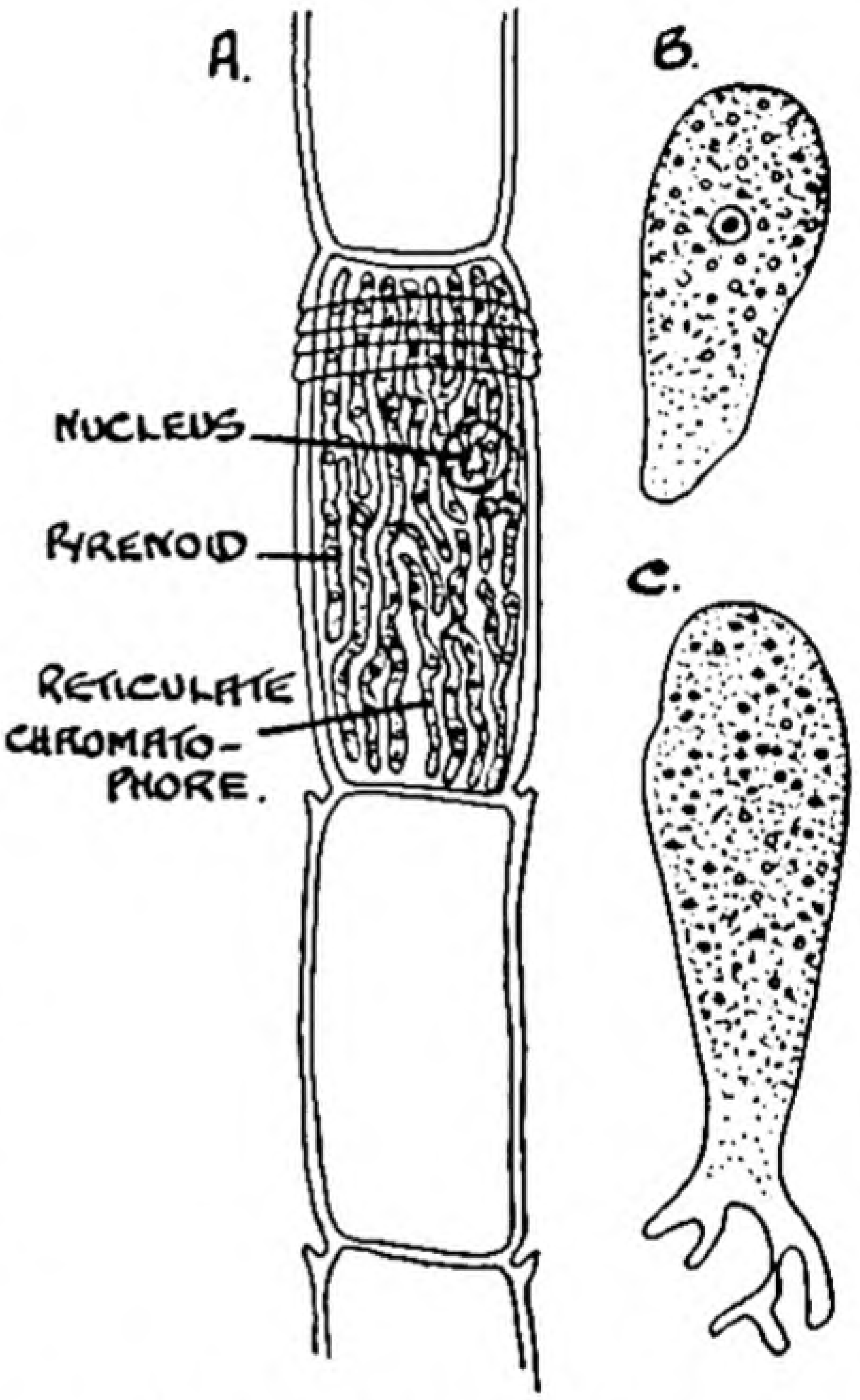

Fig. 369. *Oedogonium.*

A, Portion of plant showing one cap-cell; B and C, Young plants.

40. Structure of the Cell (Fig. 369)

The upper end of each cell in some species is more or less dilated. The cell-wall consists chiefly of cellulose; there is little or no trace of a mucilaginous sheath. Each cell contains a single large **chloroplast** consisting of a network of anastomosing bands lying in the cytoplasm. Numerous **pyrenoids** are present. There is a single **nucleus** lying usually near the middle of the cell. The "cap-cells" show a series of transverse ring-like markings at the upper end.

41. Cell-division

The way in which the growth and division of the cap-cells are effected is characteristic. A ring-like cushion is formed on the inner surface of the cell-wall near the upper end of the cell (Fig. 370, A), and the nucleus of the cell divides into two. The cell-wall then splits all round just outside the ring-like cushion. The latter is stretched and gives rise to a membrane which is intercalated in the cell-wall (**X** in Fig. 370, B).

Meanwhile a dividing wall, laid down between the two nuclei, is formed opposite the lower end of the intercalated membrane. The bounding wall of the upper cell therefore consists chiefly of the intercalated membrane; but there is a portion of the old cell-wall, fitting like a cap, at the upper end of the cell, where it produces a transverse ring-like mark.

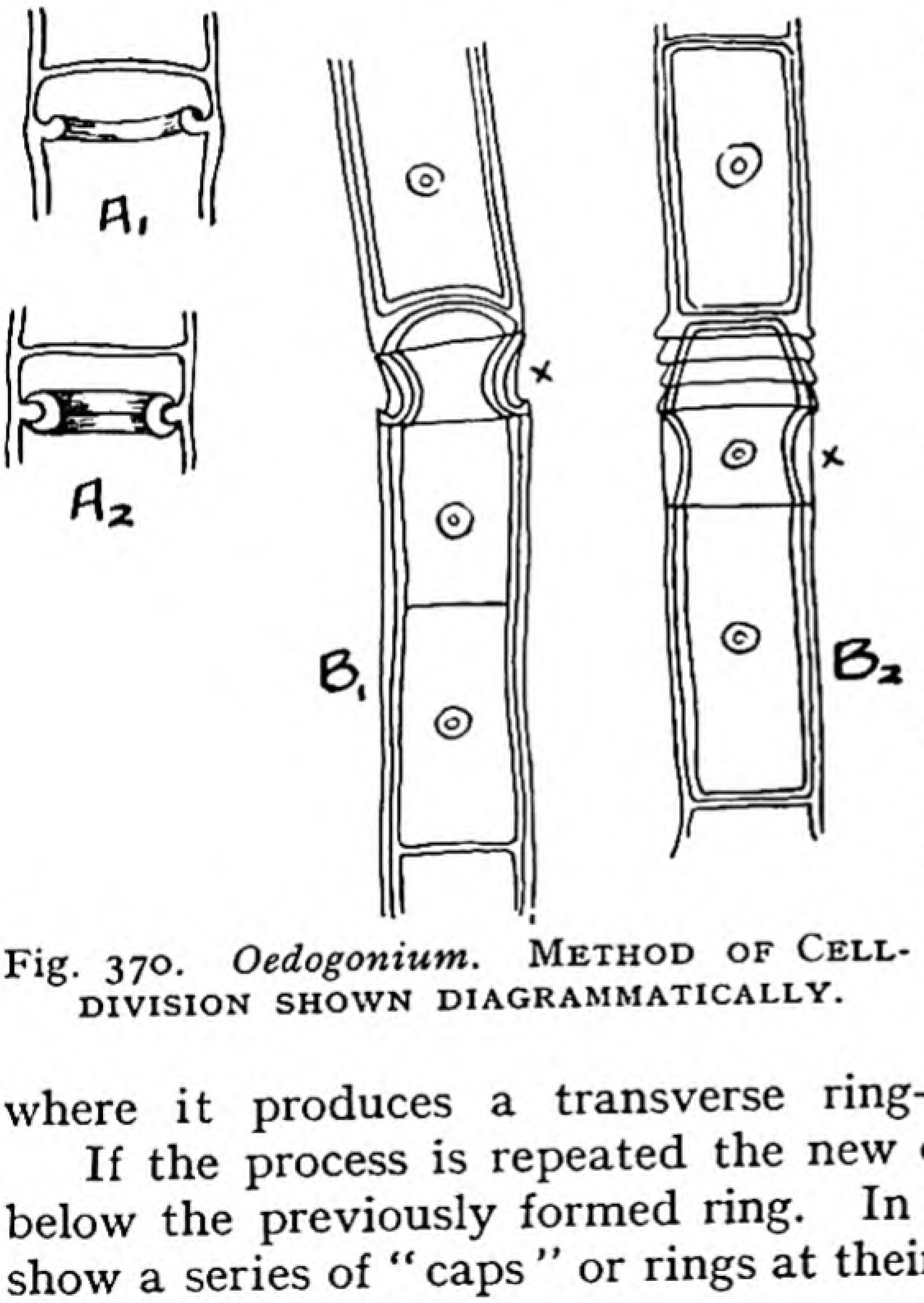

Fig. 370. *Oedogonium*. METHOD OF CELL-DIVISION SHOWN DIAGRAMMATICALLY.

If the process is repeated the new cushion arises immediately below the previously formed ring. In this way the cells come to show a series of "caps" or rings at their upper ends (Fig. 369, A).

42. Asexual Reproduction (Fig. 371, A, B)

Asexual reproduction apart from fragmentation is effected by means of zoospores. Any cell of the filament may function as a sporangium and produce a single multiciliate zoospore. The **zoospore** is set free by a rupture of the upper end of the sporangium. The zoospore is a comparatively large pear-shaped body. Its broad posterior end contains chlorophyll; its narrow end has a colourless beak round the base of which is a crown of cilia. At the time of liberation it is enclosed in a thin layer of mucilage, which soon disappears. An eye-spot is present.

After a short motile period the zoospore settles and attaches itself to some object by its anterior end. The cilia are withdrawn, a cell-wall is secreted, and a new filament formed. The basal cell in some remains short and blunt; in others it becomes pointed and may form a lobed attaching organ.

43. Sexual Reproduction (Figs. 371, B, C and 372)

The sexual organs are *oogonia* and *antheridia*. The **oogonia** are formed, usually singly, from actively growing cells. The cell undergoes a division, and the upper cell expands to form the oogonium. The lower cell forms the supporting cell, but sometimes it undergoes division and forms further oogonia. In such cases the oogonia occur in series. The oogonium becomes globular or ovoid, and its contents are rounded off to form a single **oosphere.** The oosphere contains abundant chlorophyll, but on the side where fertilisation will be effected there is a clear "*receptive spot.*" The oosphere is not set free from the oogonium. Before fertilisation either a transverse split or a pore (according to species) appears at the upper end of the oogonium and through this the spermatozoid reaches the oosphere, which it enters at the "receptive spot." Before fertilisation mucilage is extruded from the oosphere.

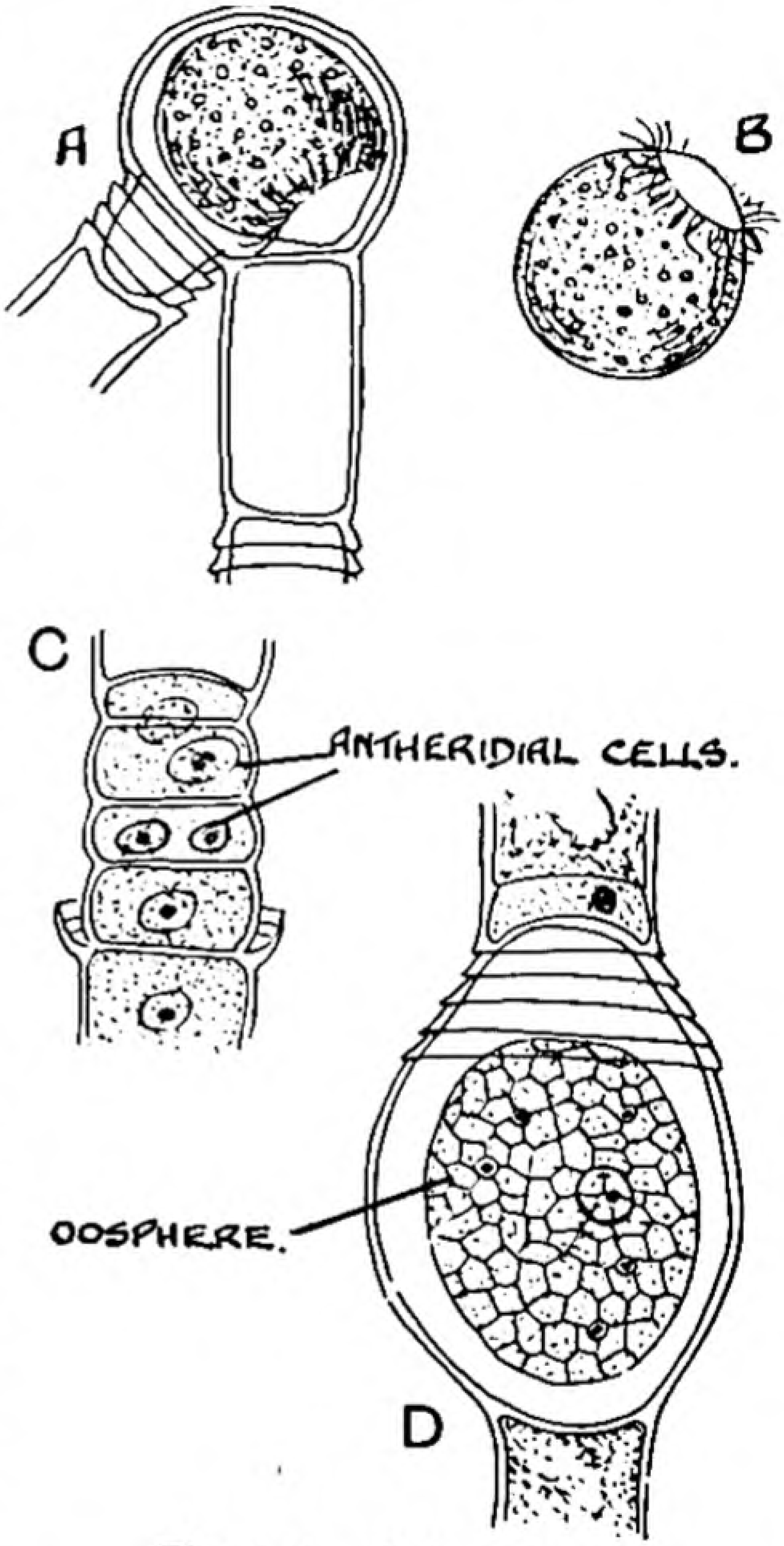

Fig. 371. *Oedogonium.*

A, Zoospore in Sporangium; B, Zoospore, liberated; C, Part of filament with Antheridia; D, Part of filament with Oogonium, containing Oosphere.

The **antheridia** are short flat cells formed by division of the ordinary cells of the filament (Fig. 371, C). Each antheridial cell by division of its contents gives rise usually to two spermatozoids, which resemble the zoospores, but are much smaller and contain less chlorophyll; they consist largely of nucleus. The spermatozoids swim freely and some finally reach the oogonia. A single spermatozoid enters the oogonium and fuses with the oosphere, and so fertilisation is effected.

Many species of *Oedogonium* are monoecious. In a few dioecious species the male and female plants are both large. In the great majority of the dioecious species the sexual reproductive processes are more specialised. The antheridia are produced on "*dwarf-male*" plants. In these dioecious species special motile spores, known as **androspores,** are produced, either by the female, or on distinct plants in **androsporangia,** which are cells resembling the antheridia, but rather larger. Each androsporangium gives rise to an androspore intermediate in size between a zoospore and a spermatozoid, but resembling these. The androspore, after a motile period, attaches itself to a female plant near, or on, an oogonium, and produces a "dwarf-male" consisting usually of a basal cell, and an antheridium (Fig. 372). Two spermatozoids are produced in the antheridium and set free by the disorganisation of the antheridial cells, or by the separation of a lid at the top.

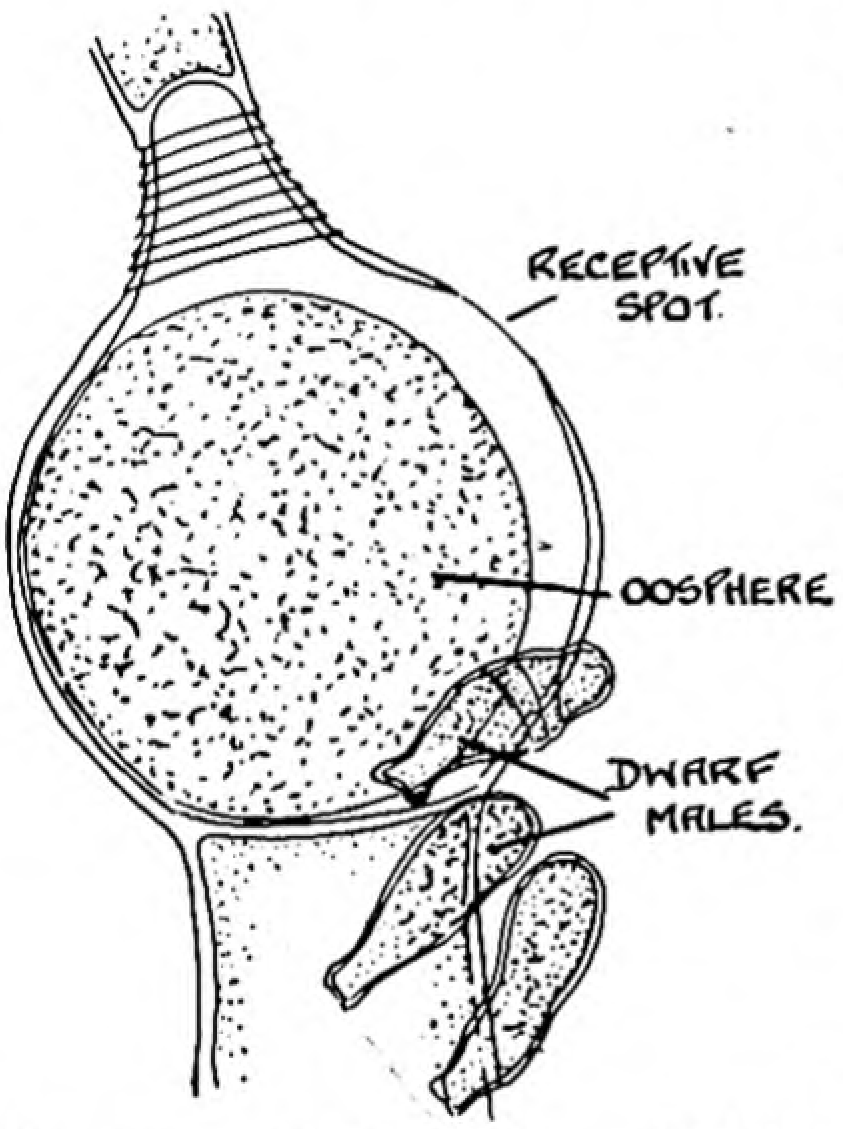

Fig. 372. *Oedogonium.* DWARF-MALES ATTACHED NEAR OOGONIUM, WHICH SHOWS RECEPTIVE SPOT.

44. Germination of the Oospore

The fertilised oosphere forms a thick cell-wall and becomes the oospore. It is at first green, but later loses its chlorophyll and becomes brown or red. It usually passes through a period of rest, but in some cases germinates directly.

It is finally liberated by the decay of the wall of the oogonium. At germination its contents undergo division into four **zoospores** exactly like those produced in the sporangia, and these grow into new *Oedogonium* filaments. Sometimes the oospore on germination first produces aplanospores, and these later liberate zoospores. Occasionally in some species the oogonia give oospheres which develop parthenogenetically and function as normal oospores, germinating to give rise to zoospores.

The *Oedogonium* plant is haploid, meiosis occurring during germination of the oospore.

The life history of a dioecious species may be graphically represented as in Fig. 373.

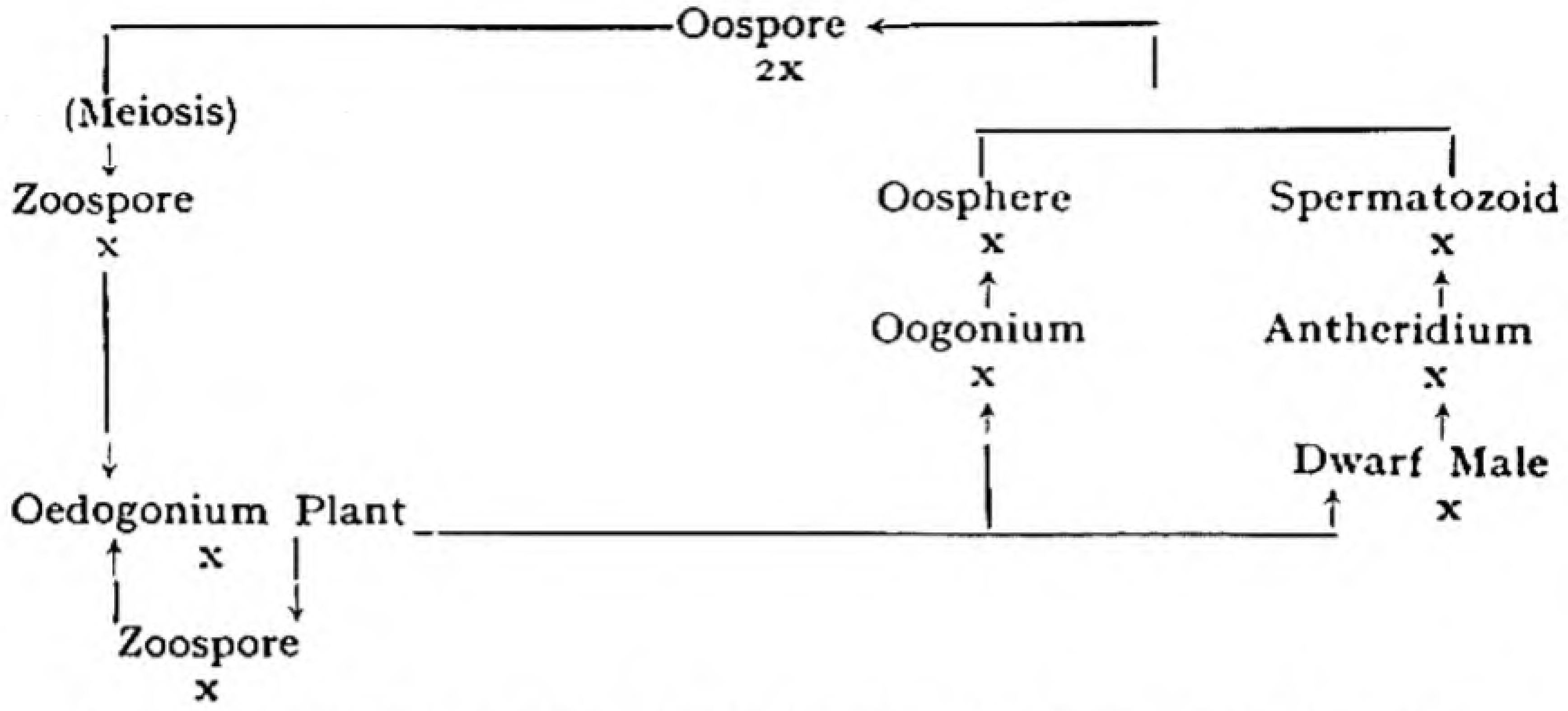

Fig. 373. LIFE HISTORY OF DIOECIOUS SPECIES OF *Oedogonium*, GRAPHICALLY REPRESENTED. (x = haploid number of chromosomes.)

FUCUS

45. General Appearance and Habit

The Phaeophyceae or Brown Algae, to which *Fucus* belongs, are with few exceptions seaweeds. In the lower forms of the Phaeophyceae the sexual reproduction is isogamous; in the higher forms, heterogamous. Many of them are small and filamentous, but the group includes some of the largest forms of Algae.

Fucus is one of the larger forms and includes several common species differing in certain minor characters. *Fucus vesiculosus* is the common bladder wrack; *F. serratus* is the serrated wrack. The plant body is a thallus which, however, shows differentiation into a basal, branched, attaching organ (hapteron), a straight, cylindrical stem-like portion, and a dichotomously branched membranous expansion (Fig. 374). It should be noted that the hapteron has no absorbing function, but only acts as a hold-fast.

Running up the middle of each flattened lobe of the thallus is a midrib formed by the thickening of the tissue in that region. In the older parts of the thallus the marginal portion dies away and leaves only the midrib. This is the mode of origin of the cylindrical stem which represents the persistent thickened midrib of the older part of the thallus. A distinct stem is not recognisable in the young plant.

Fucus inhabits the zone between low and high tide-marks. It is exposed at low tide and covered at high tide when it is subjected to the force of the waves. The strong hold-fast attaches the plant to rocks, etc., and prevents it from being washed away. The plant is preserved from injury by the pliant nature of its stalk, and the yielding, flattened character of its branches. Some species (*F. vesiculosus*) are rendered still more buoyant by the development of **air-bladders**—hollow dilations of the thallus filled with gas. The plant is protected from excessive desiccation, when exposed at low tide, by the mucilaginous character of its tissues, a protection rendered the more necessary by the absence of a cuticle.

If we examine the apices of the branches at certain periods it will be found that they are covered with small dots, and are more or less swollen (Fig. 374). These dots mark the entrance to internal flask-shaped cavities in the thallus called **conceptacles,** in which the sexual organs are developed.

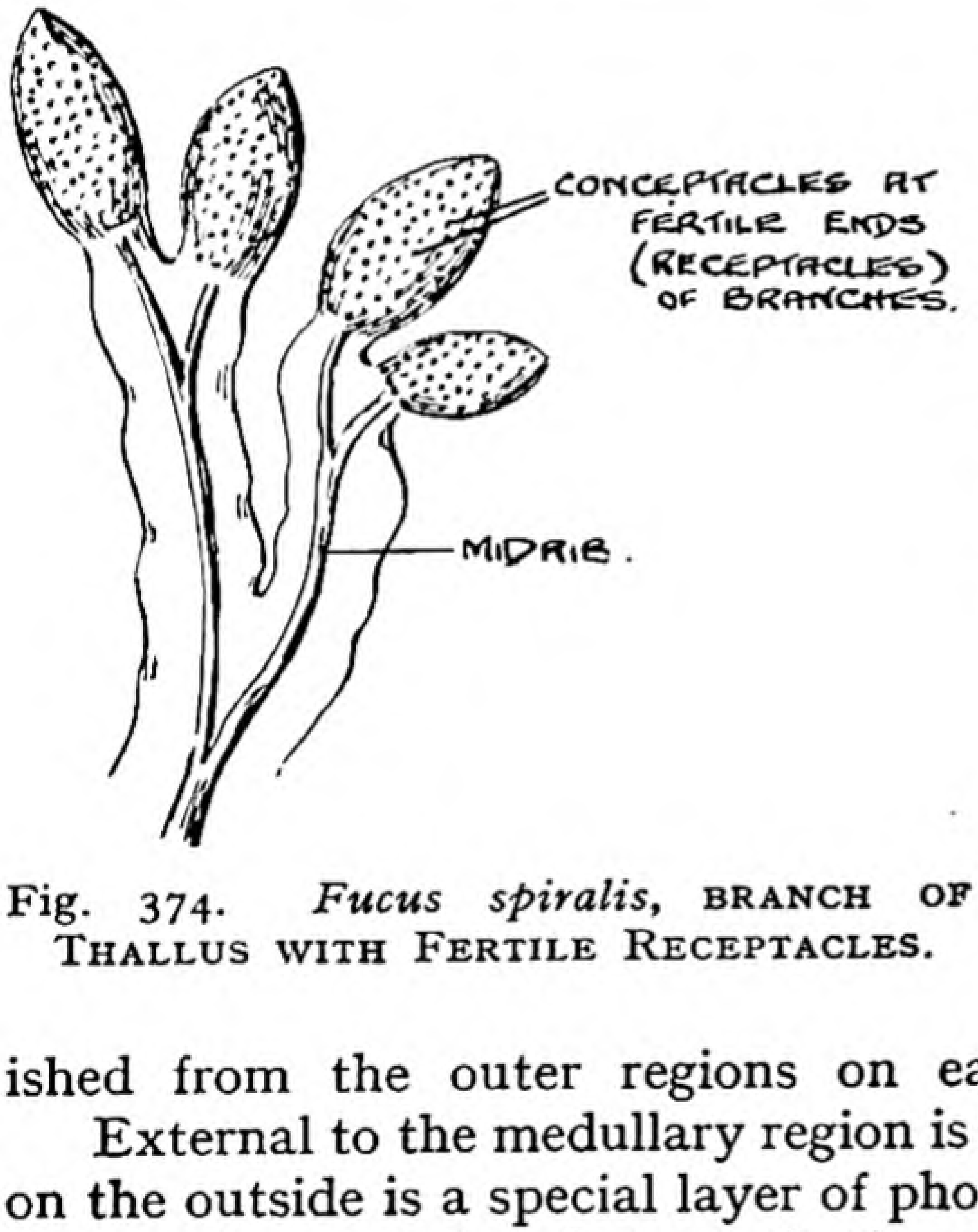

Fig. 374. *Fucus spiralis*, BRANCH OF THALLUS WITH FERTILE RECEPTACLES.

In some species, e.g. *F. serratus*, small dots are found scattered over the normal thallus. These mark the position of pits in which hairs are developed, and which may be regarded as sterile conceptacles.

46. Structure and Growth of the Thallus

A section, passing through both surfaces and taken at any part of the thallus, will show that a central or **medullary region** of tissue can be distinguished from the outer regions on each side (Fig. 375).

External to the medullary region is the cortex and bounding this on the outside is a special layer of photosynthetic cells. The outer limiting layer of the photosynthetic zone consists of tightly packed cells that are meristematic, and by their division add to the photo-synthetic tissue. These photosynthetic tissues contain chromatophores in which the brown pigment fucoxanthin is present in addition to chlorophyll. The presence of chlorophyll in *Fucus* is readily demonstrated by immersing a piece of thallus in warm water. The water extracts the fucoxanthin and the chlorophyll remains so that the thallus appears green. The innermost layer of photosynthetic cells is also meristematic and by the division of these cells the tissue of the cortex is continually being augmented.

The cortex consists of large cells which probably store the products of photosynthesis, which, in *Fucus*, do not consist of starch but of another complex carbohydrate. The central medullary region consists of an interlacing network of filaments, or medullary hyphae, with thick mucilaginous walls. Meristematic activity on the part of the innermost cells of the cortex gives rise to additional medullary hyphae. The medullary hyphae constitute a conducting tissue. There is in *Fucus* a marked division of labour, so that photosynthesis, storage, and conduction are functions all carried out by special tissues. There is, however, no tissue-differentiation comparable with that shown by the higher vascular plants.

At each growing point of the thallus there is a single large **initial cell** which has the form of a four-sided truncated pyramid. The segments from the base of this cell form medullary hyphae, those from the sides form cortex and photosynthetic tissue. At each branching the apical cell divides into two (true dichotomy), and each segment becomes the apical cell of a branch. Their growth rate may, however, be unequal, and one branch more vigorous than the other.

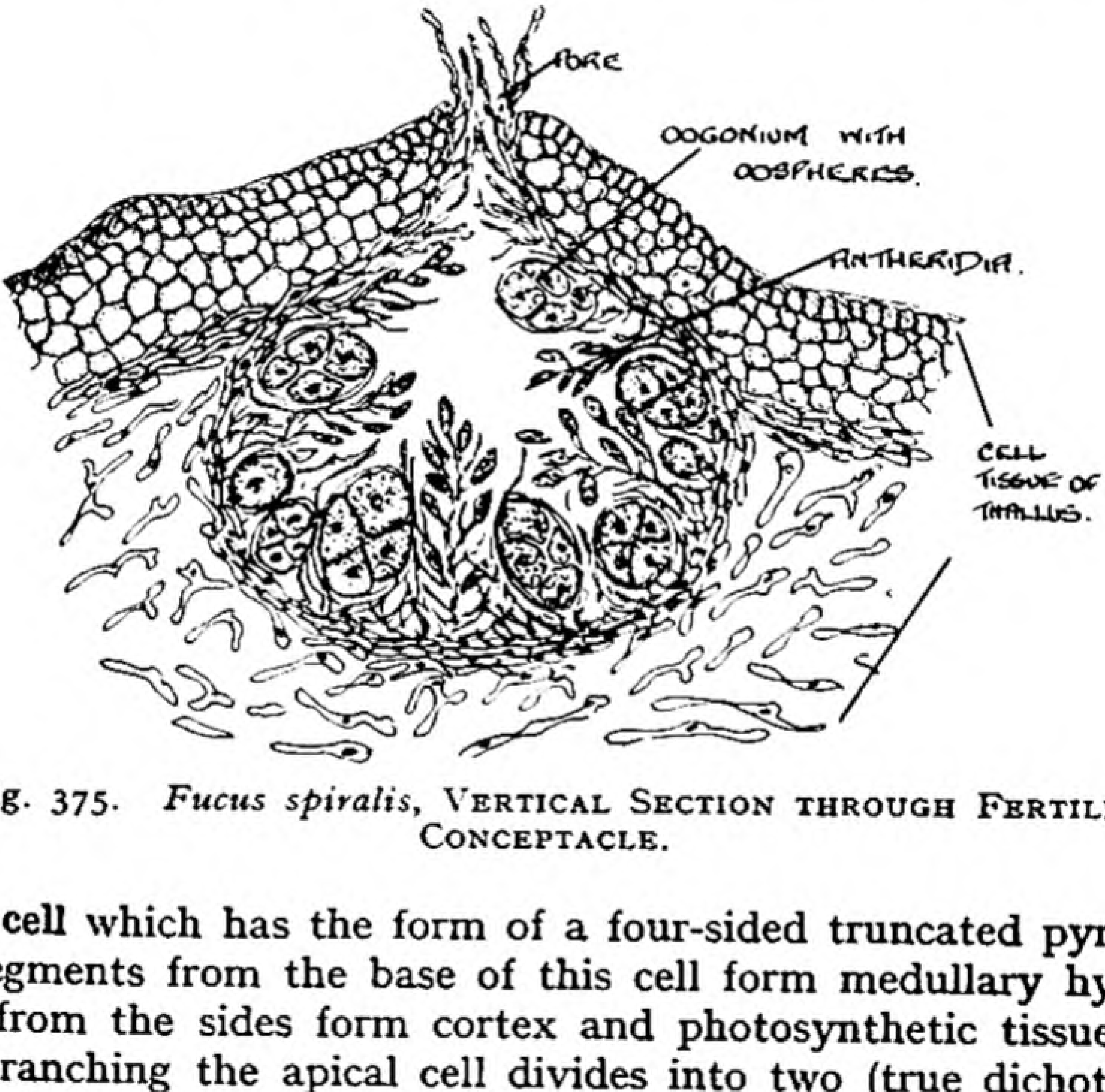

Fig. 375. *Fucus spiralis*, VERTICAL SECTION THROUGH FERTILE CONCEPTACLE.

47. Reproduction

There is no special method of asexual reproduction in *Fucus*, but sometimes adventitious branches, formed at the base of the thallus by the activity of the cortical meristem, may be separated off and form new plants. **Sexual reproduction** is common. The sexual organs are contained in the conceptacles mentioned above. Each **conceptacle** (Fig. 375) opens on the surface of the thallus by a minute aperture called the **ostiole.** Numerous multicellular **hairs** are developed from the cells lining the conceptacles. Many of these form paraphyses; others bear the sexual organs.

In the development of a conceptacle one or several superficial cells of the thallus cease to grow and become disorganised. The surrounding tissue grows vigorously, and soon encloses a flask-shaped cavity.

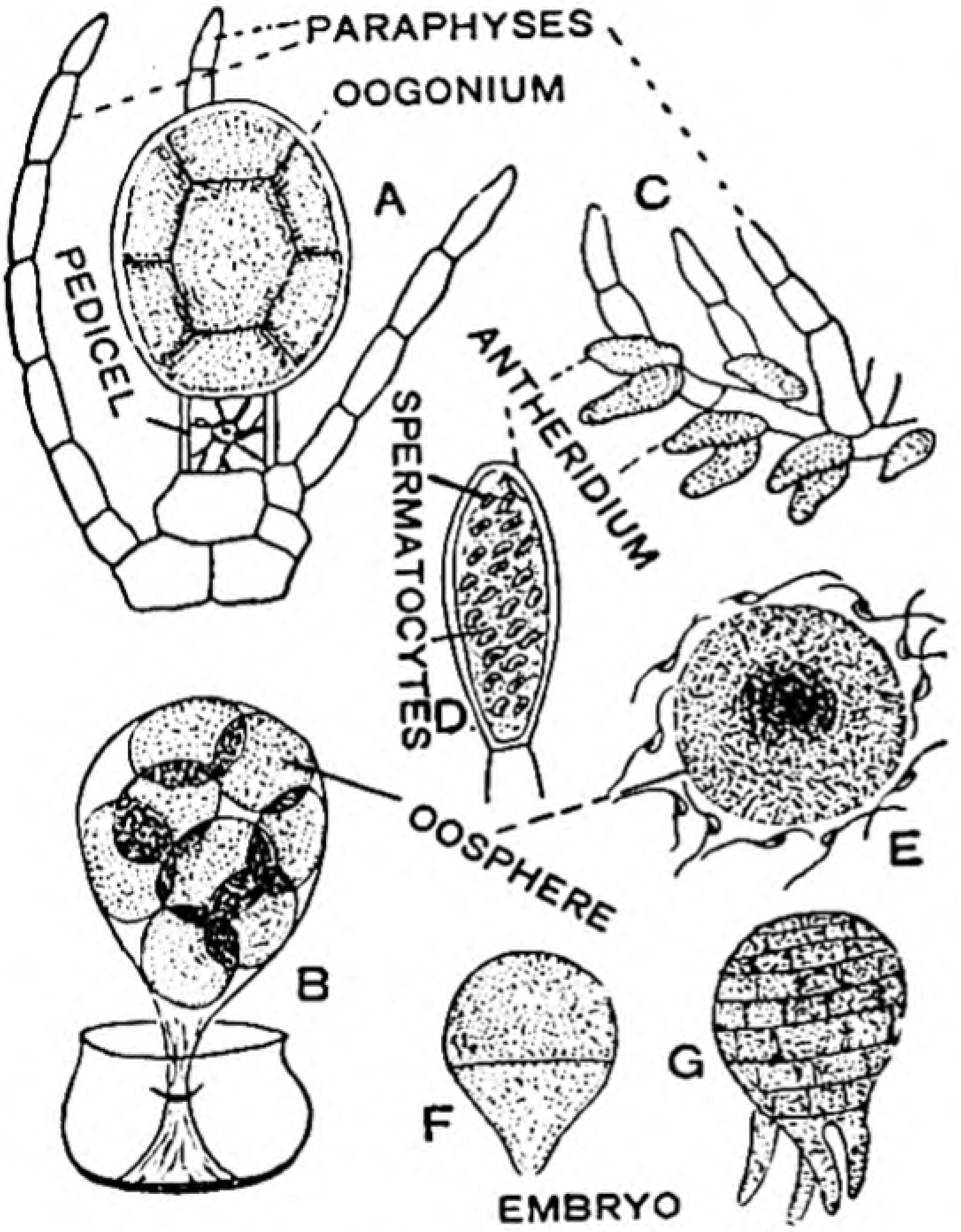

Fig. 376. *Fucus vesiculosus.*

A, Oogonium with contents segmented; B, Oospheres partly liberated; C, Antheridia on branched filament; D, Antheridium containing spermatocytes; E, Oosphere being fertilised; F and G, Segmentation of germinating oospore.

48. The Sexual Organs (Fig. 376)

The sexual organs are antheridia and oogonia. The **antheridia** are borne in clusters, and are on the branches of much-branched hairs. Each antheridium is developed from a single cell. When fully formed it is a small, ovoid, orange-coloured sac, the wall of which consists of two thin membranes. The contents have undergone division to form a large number (usually 64) of biciliate **spermatozoids.** The cilia, of unequal length, are developed laterally, the shorter one is directed forwards and the other backwards, and each spermatozoid has an orange-coloured **chromatophore.**

The **oogonium** is a much larger, dark-coloured structure. It also is developed from a single cell. It is borne on a short unicellular stalk. Its wall also consists of two membranes and its contents divide to form eight **oospheres.**

Many species of *Fucus* are *dioecious,* e.g. *F. vesiculosus,* recognised by its bladders, and *F. serratus,* recognised by its serrate margin; but in *F. spiralis* the sexual organs are borne on the same plant and in the same conceptacle.

49. Fertilisation (Fig. 376, E)

When the spermatozoids are ripe they are discharged from the antheridium in a mass still enclosed within the inner layer of the antheridial wall. Similarly the outer membrane of the oogonium opens at its apex and the mass of eight oospheres is liberated, still enclosed within the inner membrane. This generally takes place when the plants are exposed at low tide. The hairs of the conceptacle secrete mucilage which oozes out of the ostiole, carrying with it the sacs of spermatozoids and oospheres. When the tide rises again the spermatozoids are set free from their sac, and the oospheres also from theirs by the thin membrane breaking down at one end and partly turning inside out. The oospheres are passive. Numerous spermatozoids cluster round each oosphere. They are probably attracted to it chemotactically, and as they swim around it the lashings of their cilia set up currents in the water which cause the oosphere to rotate. Finally, one spermatozoid enters the oosphere and the two nuclei fuse. After fertilisation the oosphere becomes invested with a cell-wall and the oospore thus formed proceeds to germinate immediately.

50. Germination of the Oospore (Fig. 376, F, G)

The oospore becomes somewhat pear-shaped and a transverse wall divides a narrow basal cell from a broader, upper one. The former gives rise to a much-branched hapteron, the latter, by further division, gradually develops into the thallus.

51. Meiosis in Fucus

It is found that the *Fucus* plant is diploid. Meiosis takes place at the first nuclear divisions of the developing antheridium and oogonium. The gametes are therefore haploid, and the diploid condition is restored in the fertilised oosphere. The life-history of *Fucus* is graphically represented in Fig. 377.

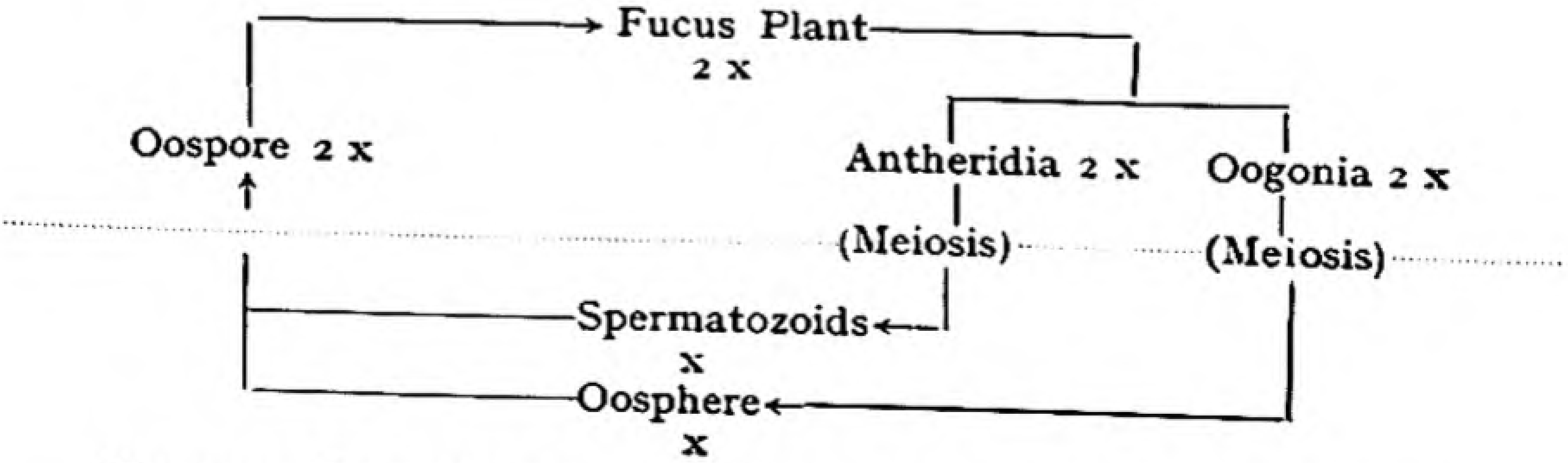

Fig. 377. LIFE HISTORY OF *Fucus*, GRAPHICALLY REPRESENTED.
(x = haploid number of chromosomes.)

CHAPTER XX

FUNGI, BACTERIA, AND VIRUSES

1. General

The Fungi constitute the second important Class into which the Thallophyta are subdivided. They are readily distinguished from the Algae by the want of chlorophyll; starch also is entirely lacking. This *by itself* would not be a sufficient reason for separating the two classes. If this were all, we might, with equal reason, separate those few Spermatophyta which have no chlorophyll from the rest. The Fungi, however, as a whole, are further distinguished by special characters in their structure, development, and life history.

2. The Mycelium

The typical vegetative structure of the Fungi is a filamentous and much-branched thallus called a *mycelium*. The filaments or threads of which the mycelium consists are called **hyphae.** Sometimes we find more massive structures, more especially in the parts bearing the reproductive organs. When we examine these, however, we find that they consist of hyphae woven together so as to form a **false tissue,** or pseudo-parenchyma, *i.e.* a tissue formed, not by the division of cells all originally connected with each other (true tissue), but by the interweaving of separate hyphae. Occasionally a weft of fungal hyphae forms a compact root-like strand, a rhizomorph, or gives rise to a compact resting body, a sclerotium, whose outer cells form a hard protective layer. Sometimes the plant-body consists of a single cell only, as in the various forms of yeast.

The mycelium may be septate or non-septate. When non-septate it is coenocytic; even where it is septate the different segments may contain several nuclei, and be coenocytic. The segments in the higher Fungi, however, usually contain only one or two nuclei. The cell-walls of most Fungi consist of cellulose, or of a special type of cellulose known as fungal cellulose. In the hyphae or their segments there is a lining layer of cytoplasm surrounding a central vacuole. The nuclei are small. Oil may be present as a storage substance, and sometimes protein bodies are found. Although starch is absent from the cells, another complex polysaccharide, *glycogen*, is often present.

3. Nutrition

The Fungi differ fundamentally from normal green plants in their mode of nutrition. Since chlorophyll is lacking they are unable to synthesise carbohydrates from carbon dioxide and water.

They derive their organic food-material from complex carbon compounds which they obtain from external sources. They are able to absorb only soluble compounds and the hyphae secrete enzymes which convert insoluble substances to soluble ones, which are then absorbed. Although the Fungi are unable to synthesise sugars from carbon dioxide, they can synthesise from soluble sugars the more complex carbohydrates which go to form their cell-walls. Similarly, if supplied with carbohydrates and relatively simple nitrogenous compounds such as ammonium salts, they are able to synthesise proteins and eventually protoplasm. Ammonium salts do not represent the only possible source of nitrogen. Many complex but soluble organic nitrogenous compounds can also be absorbed and utilised.

4. Mode of Life

Fungi usually live either as parasites or as saprophytes. Some are not confined to one mode of life, but may live as parasites or as saprophytes, according to circumstances. In a parasitic Fungus the hyphae may penetrate the living cells of the host, or simply ramify between the cells. The power of penetrating and disorganising cell-walls which such hyphae frequently possess is due to the secretion, at the tips of the hyphae, of an enzyme which acts on cellulose. The whole of the mycelium may be absorptive, but some parasites, whose hyphae ramify between the cells of the host, develop special absorbing organs (*haustoria*) which penetrate the cell-walls and enter the cells.

The parasitic Fungi may derive their nutriment from other Fungi, from Algae and other green plants, or from animals (including man), and may be the cause of disease in the organisms which they parasitise. When they attack plants of agricultural or horticultural importance serious reductions in yield may result. Those parasitic Fungi which parasitise the skin and dermal appendages of animals (especially man) are collectively referred to as dermatophytes. They may be the cause of certain diseases (e.g. ringworm). A few Fungi establish with other plants relationships that are not entirely of the nature of parasitism. They form an association from which the host plant derives benefit. We shall have occasion to refer to symbiotic associations of this nature later in the chapter, whilst some have already been described.

The hyphae of a saprophyte grow either in dead plant or animal remains, or on organic waste products, or stores of organic material, or less frequently in nutritive solutions.

5. Reproduction and Life History

There appears to be little doubt that the Fungi were originally derived from algal forms—that the ancestral types were, in fact, Algae which assumed a dependent mode of life, and lost their chlorophyll. As supporting this view, we find that in the lower forms of Fungi, the Phycomycetes, to which *Mucor* and *Pythium* belong, there is a close resemblance to certain Green Algae like *Spirogyra* or *Vaucheria*. Their sexual reproductive organs are very similar, and frequently also their general structure presents a close resemblance. The other groups of Fungi, the Ascomycetes and Basidiomycetes, diverge widely from the Algae and possess very special characters.

The occurrence of functional sexual organs in some of the Ascomycetes has now been established. In many Ascomycetes and Basidiomycetes true sexual reproduction does not occur, although sexual organs may be formed.

The higher Fungi have a mode of life well suited to aerial conditions. In the lower groups, however, certain stages in the life history are dependent on the presence of " free " water. A few of the Fungi have ciliated zoospores and gametes that can swim freely. The occurrence of ciliated swimming spores and gametes is looked upon as the retention of an ancestral character more typical of aquatic than land plants.

There is in the Fungi no fixed and regular alternation of generations corresponding to the alternation in the higher plants.

6. Classification

The Fungi are divided into the following main groups:—

A.—Those in which the mycelium is usually well developed and non-septate, the **Phycomycetes.** These are further subdivided according to their mode of sexual reproduction—if isogamous, producing zygospores, **Zygomycetes,** if oogamous, producing oospores, **Oomycetes.**

B.—Those in which the mycelium is septate. These are further classified into **Ascomycetes,** where the characteristic spores are endogenous, *i.e.* produced in a sac called an ascus; **Basidiomycetes,** where the characteristic spores are exogenous, *i.e.* borne externally on a basidium; **Fungi Imperfecti,** which produce neither ascospores nor basidiospores. These last-named are probably, in the main, modified Ascomycetes, and types whose complete life history is as yet not known.

A certain number of organisms which are not true Fungi, though in certain respects resembling them, constitute the **Myxomycetes.** At some stage in their development the plant body consists of a naked mass of protoplasm. The same is true of other " Slime Fungi " such as the one which produces the disease known as club-root in plants of the genus *Brassica*.

The types whose structure and life history we now proceed to describe will serve to illustrate most of the above points.

MUCOR

7. Structure and Mode of Life

Mucor is one of the commonest of those Fungi which are called " moulds." In its mode of life it is a saprophyte, and grows on many different kinds of organic substance. It can readily be obtained if bread which has been soaked in water, is kept under cover for four or five days at a moderate temperature. It makes its appearance in the form of little white patches, which gradually spread and unite. A common species is *M. Mucedo*.

The **mycelium** (Fig. 378) is copiously branched. It ramifies in the organic substance on which the Fungus is growing, and absorbs nourishment from it. The branches, or **hyphae,** get finer and finer the deeper they pass into the substratum. The structure of the mycelium can readily be made out if a portion of it is mounted in water on a slide, and examined under the microscope. The finely granular protoplasm contains small vacuoles and oil-globules. With special methods of preparation the presence of numerous small nuclei can be demonstrated. In an actively growing mycelium there are no septa, although these may occasionally be found in old cultures. The mycelium, therefore, does not consist of definite cells, but is coenocytic.

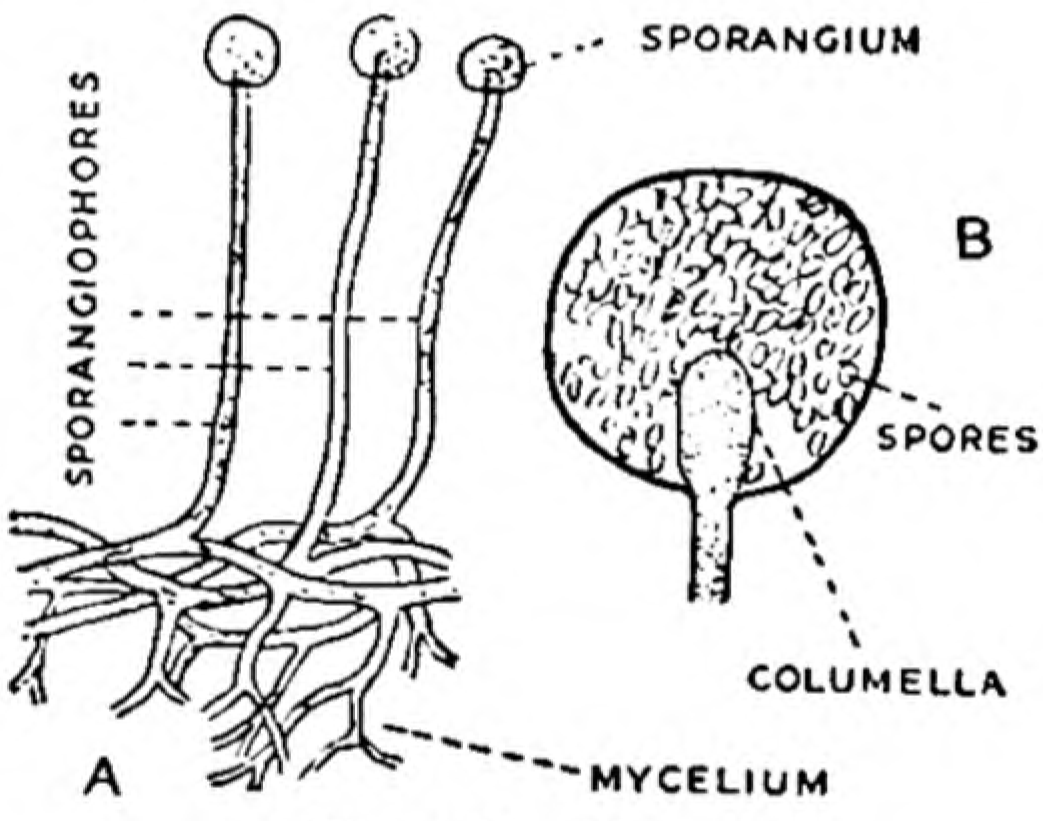

Fig. 378. *Mucor.*

A, A portion of a mycelium bearing sporangiophores; B, A single sporangium.

8. Asexual Reproduction (Fig. 378)

This is effected by means of small ovoid spores. If some actively growing *Mucor* is examined, rather stout aerial branches will be found springing from the surface of the mycelium. Each bears at its tip a spherical sac, which is a sporangium. The branches bearing the sporangia appear to be negatively geotropic and negatively hydrotropic. They therefore grow upwards, partly because of gravity stimulus, and partly because their negative hydrotropism causes them to grow away from the wet substratum on and in which the *Mucor* mycelium is growing. The sporangium is formed by the swelling of the upper end of the aerial branch. It is cut off from the lower portion, the sporangiophore, by a dome-shaped septum, which protrudes into the sporangium to form a structure called the **columella.** As the sporangium ripens it becomes black. Its wall is studded with spicules of calcium oxalate.

The spores are developed inside this sporangium by division of the protoplasmic contents; they are multinucleate. Both sporangium and columella absorb water and swell and finally the sporangium-wall bursts, so that the spores are liberated and become distributed. In the dehisced sporangium the more or less colourless columella may be somewhat globular, like the undehisced sporangium, and may have the remains of the sporangium-wall persisting round its base. Each spore which falls on a suitable substratum puts out a germ-tube and forms a new mycelium.

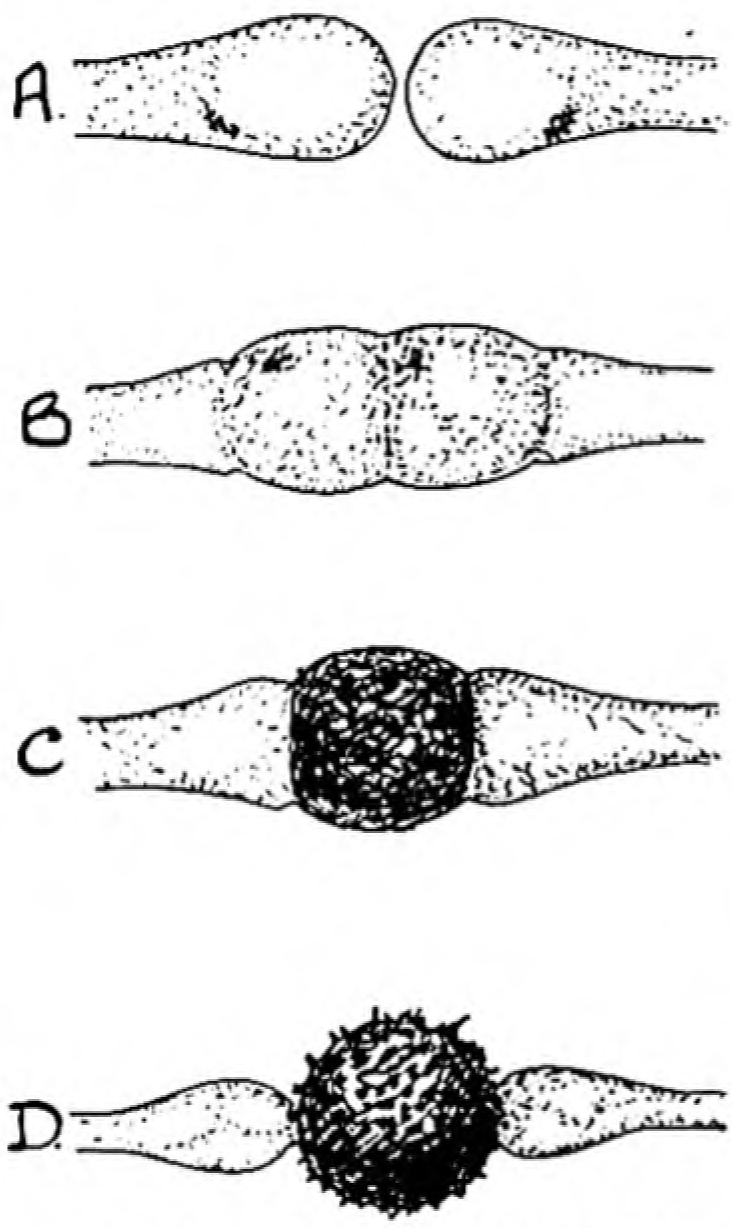

Fig. 379. *Mucor.* CONJUGATION. FOUR STAGES IN THE FORMATION OF A ZYGOSPORE.
A, Lateral protuberances from long filaments; B, Gametangia in contact; C, Fusion; D, Zygospore.

9. Sexual Reproduction

Sexual reproduction may occur when two young actively growing branches come into contact, either laterally, or far less frequently, at their ends. When the long branches are in close contact, small lateral protuberances are formed, which, while attached at the tips, grow in length and gradually push the original long hyphae apart. The terminal part of each short lateral branch is cut off by a septum to form a **gametangium.** A number of paired gametangia may be formed in a row between the two original long hyphae. The contents of each gametangium constitute a multinucleate **gamete.** The walls of contact between two gametangia are broken down, the gametes intermingle, and their nuclei eventually fuse in pairs. The surrounding wall becomes much thickened, dark-coloured, and warty on its surface, and the formation of the **zygospore** is complete (Fig. 379).

It has been shown for certain species of *Mucor* (*M. Mucedo*, *M. hiemalis*) that sexual reproduction will only occur between two strains which are morphologically very similar, but physiologically different. These strains are distinguished as plus (+) and minus (−), and the condition is known as heterothallism. Occasionally, slight morphological differences exist, such as one strain growing more actively and giving rise to a more luxurious mycelium than the other.

Sometimes gametangia develop into thick-walled azygospores without fusion.

10. Germination of the Zygospore (Fig. 380)

The thick-walled zygospore usually undergoes a period of rest of several months, during which it is able to withstand extremes of temperature and drought. When it germinates water is absorbed, the thick outer wall is ruptured and a hypha emerges which at once produces a sporangium. During this process of germination, meiosis takes place and nuclei of the (+) and (−) strains are segregated, becoming associated with cytoplasm and forming uninucleate spores whose strain is thus already determined. Grown individually these spores produce one strain of mycelium bearing only sporangia, but brought together the two strains produce zygospores. Each strain may be regarded as unisexual, but there is no apparent distinction between the sexes. They can only be differentiated experimentally by their power to produce zygospores on being brought together with their opposite strains.

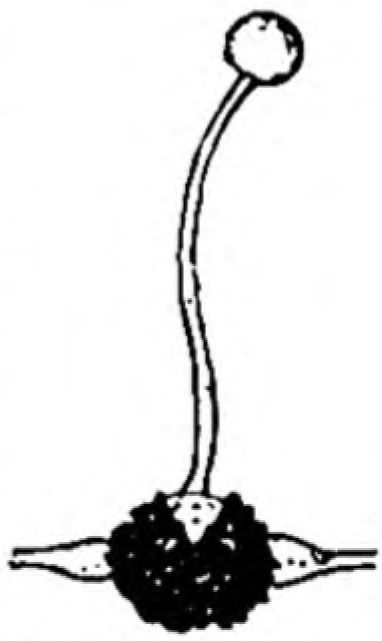

Fig. 380. *Mucor*. GERMINATION OF ZYGOSPORE TO FORM SPORANGIUM.

11. The Torula Condition

If the mycelium of *Mucor* is immersed in a nutritive solution, it may break up, by the formation of septa, into chains of cells. These cells are sometimes thick-walled, and are resting-cells (chlamydospores), which, under normal conditions, would produce new mycelia. Frequently, however, they are thin-walled oidia. In this case they separate from each other and, like yeast cells, are capable of budding and producing alcoholic fermentation in a sugar solution. This is known as the "torula" condition of *Mucor*.

12. Taxonomic Position

Mucor belongs to the group of Phycomycetes known as Zygomycetes, in which there is isogamous sexual reproduction.

PYTHIUM

13. Structure and Mode of Life

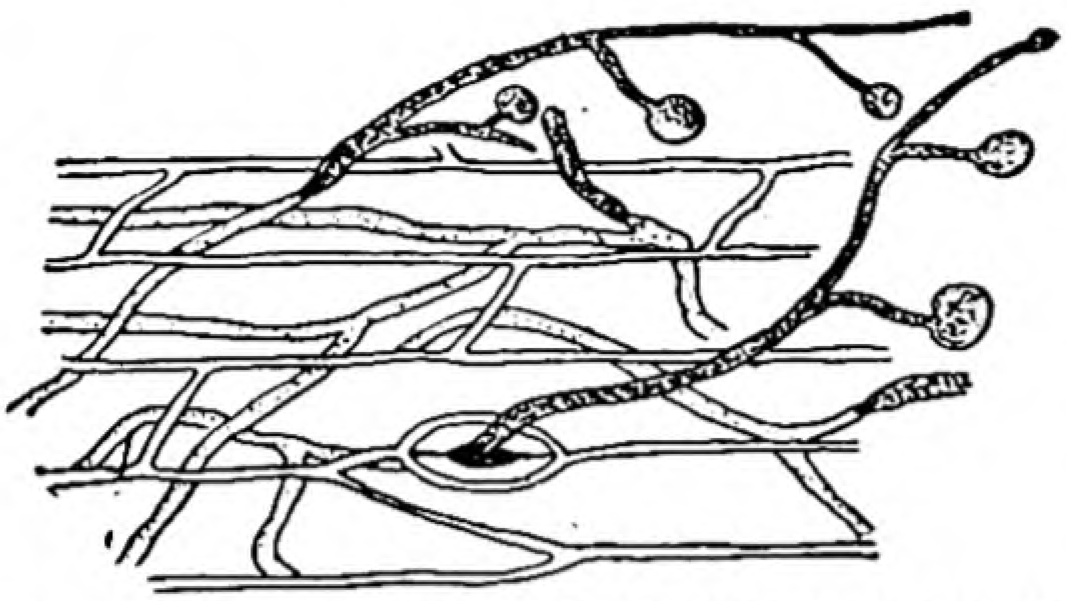

Fig. 381. *Pythium.* FREE HYPHAE BEARING ASEXUAL REPRODUCTIVE ORGANS. OTHERS IN TISSUE OF HOST OR EMERGING FROM STOMA.

If cress (*Lepidium sativum*) or certain other seedlings are grown close together under very moist conditions, it is found that they suffer from the disease known as "damping off." The first signs of infection are seen at certain points, where the seedlings collapse at soil level. From these points the disease spreads in ever widening circles. Examination shows that the collapse of the seedlings is due to destruction of the cortex, which contains numerous fungal hyphae. The disease may be caused by several Fungi, but one of the commonest species of *Pythium,* e.g. *Pythium de Baryanum* is perhaps the most usual cause of "damping off." Microscopic examination of a diseased seedling reveals the presence of the fungal hyphae in the tissues of the plant and in moist conditions the spread of the hyphae from plant to plant over the surface of the soil can be seen with the naked eye. If the atmosphere surrounding the seedlings is relatively dry the spread of the Fungus (and hence of the disease) across the soil from plant to plant is prevented. Adequate ventilation and the prevention of excessively moist conditions provides a control of the disease.

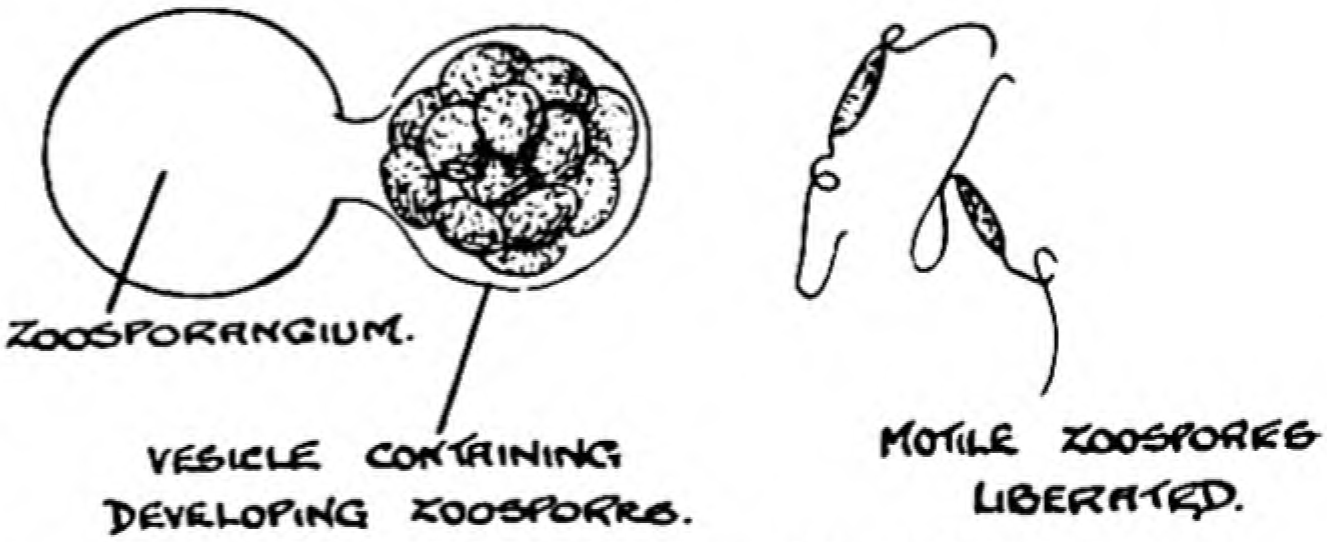
ZOOSPORANGIUM.
VESICLE CONTAINING DEVELOPING ZOOSPORES.
MOTILE ZOOSPORES LIBERATED.

Fig. 382. *Pythium intermedium.* Asexual reproduction.

The fungal hyphae which are parasitic on the seedlings grow both in the cells and in the intercellular spaces. They absorb food-materials from the host, the tissues of which are finally reduced to a dark-coloured putrefying mass, on which the Fungus continues to live saprophytically.

The **mycelium** of *Pythium* (Fig. 381) is a much-branched, non-septate coenocyte (cf. *Mucor* and *Vaucheria*). Its protoplasm contains numerous small nuclei and oil-globules.

14. Asexual Reproduction (Figs. 381 and 382)

If a diseased seedling is placed in a watch-glass in water and kept under observation, it will be found that the ends of some of the hyphae, which grow out from the surface of the plant, or of small branches of these, swell up and become globular. These globular swellings are cut off from the hyphae by cross walls. They are asexual reproductive organs and their subsequent development depends upon external conditions.

If there is an abundance of moisture each globular swelling functions as a zoosporangium and puts out a small process which swells to form a vesicle. The contents of the zoosporangium undergo cleavage and migrate into the vesicle, where they develop into zoospores. Later the vesicle ruptures, the biciliate zoospores are liberated, and swim freely in water. If a zoospore finally comes to rest on a suitable seedling, it forms a germ-tube which enters the seedling either through a stoma, or by piercing the wall of an epidermal cell, and gives rise to a new mycelium. If, however, there is a shortage of water, the potential zoosporangium functions as a spore or conidium, and sends out a germ-tube which gives rise to a new mycelium directly.

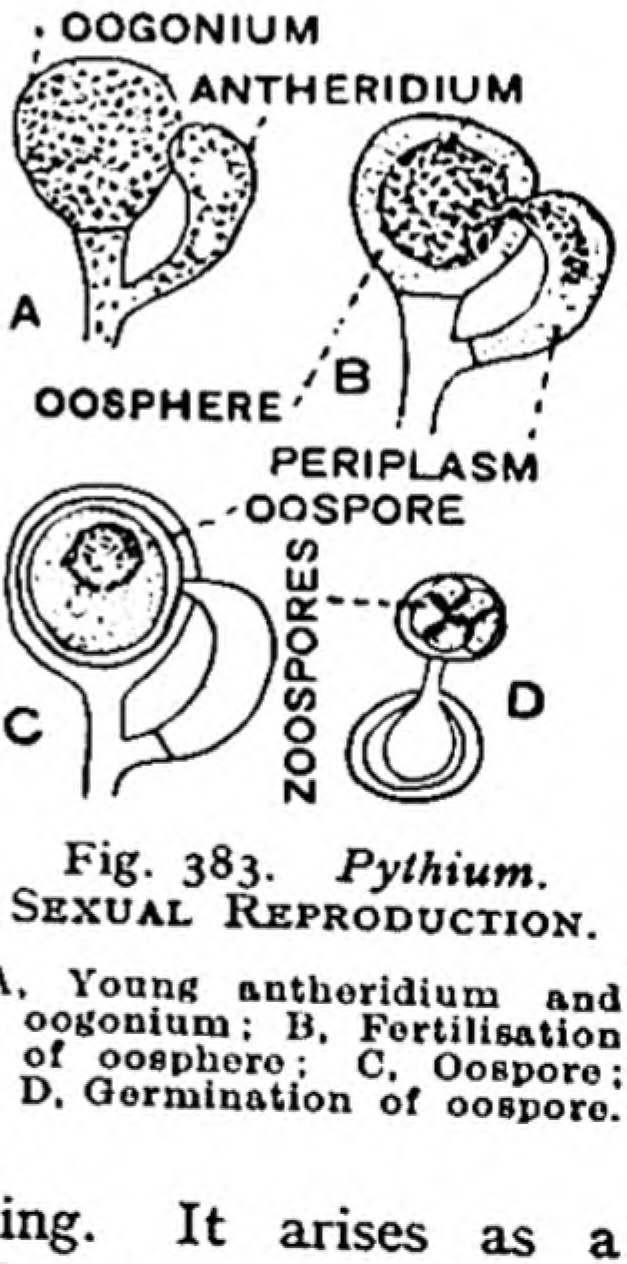

Fig. 383. *Pythium.* SEXUAL REPRODUCTION.

A, Young antheridium and oogonium; B, Fertilisation of oosphere; C, Oospore; D, Germination of oospore.

15. Sexual Reproduction (Fig. 383)

Sexual organs are produced after the host has been killed, and *Pythium* is living saprophytically on the dead tissues.

The female organ is an **oogonium.** It is usually formed on the end of a hypha in the tissues of the dead seedling. It arises as a globular swelling of the hypha, and bears a close resemblance to the asexual reproductive organ. It is cut off by a septum from the rest of the hypha. At first the protoplasmic contents have many nuclei, but soon a central region containing one nucleus, constituting the **oosphere,** is marked off from a peripheral region, called the **periplasm,** and containing the other nuclei.

The male organ, the **antheridium,** is developed on a branch which arises either on the same hypha as the oogonium, or on another hypha. It is cut off from the main branch by a septum, and its protoplasmic contents which are multinucleate are differentiated into a central portion, the **male gamete** with a single nucleus, and a peripheral periplasm. The male gamete has no cilia and is not, therefore, a spermatozoid.

The antheridium is more or less club-shaped. It applies itself closely to the oogonium, and develops a tubular process, the **fertilisation-tube,** which pierces the wall of the oogonium and through which the male gamete passes to the oosphere. This process can readily be observed in *Pythium.* The fertilised oosphere forms a thick wall and becomes the **oospore.** The outer layer of the wall is formed from the periplasm.

The oospores are essentially resting spores. They usually remain inactive during the winter and germinate in the following spring. Because of this seedlings grown on the same ground as seedlings attacked the previous year are very liable to the disease. When the oospore germinates it sends out a hypha which produces either conidia or zoosporangia, which then infect fresh seedlings. Meiosis occurs during germination.

16. Taxonomic Position

Pythium belongs to the group of Phycomycetes known as Oomycetes, in which the sexual reproduction is heterogamous. The close resemblance between the structure of the mycelium and the reproductive organs of *Pythium,* and the thallus and reproductive organs of *Vaucheria* should be carefully noticed.

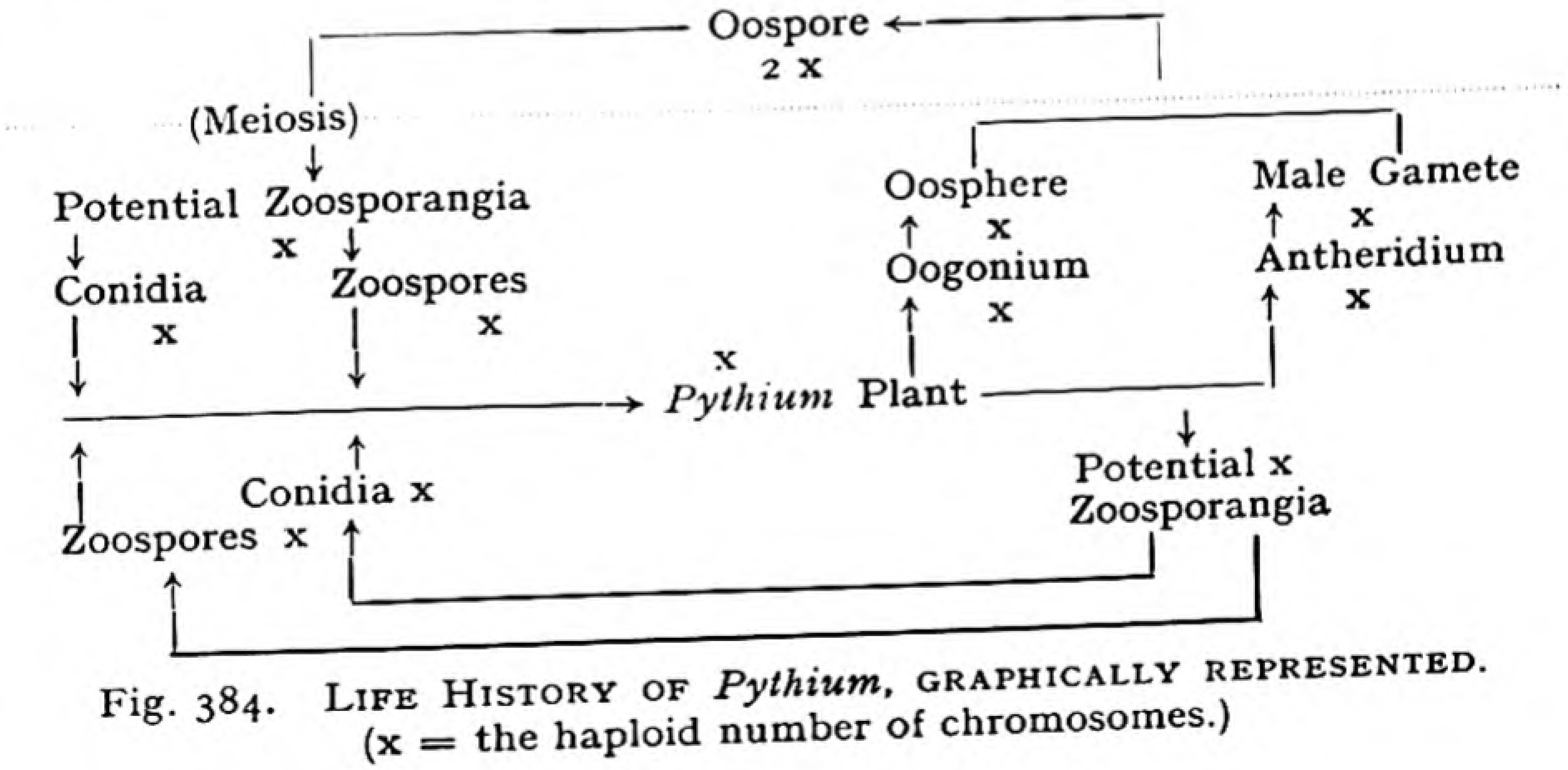
Oospore
2 x
(Meiosis)
Potential Zoosporangia
x
Conidia
x
Zoospores
x
Oosphere
x
Oogonium
x
Male Gamete
x
Antheridium
x
x
Pythium Plant
Conidia x
Zoospores x
Potential x
Zoosporangia

Fig. 384. Life History of *Pythium*, graphically represented. (x = the haploid number of chromosomes.)

Cystopus and Peronospora

17. General

The several species of **Cystopus** and **Peronospora** are, like *Pythium,* members of the Oomycetes. They differ, however, in several respects from *Pythium.*

18. Structure and Mode of Life

Like *Pythium*, *Cystopus* is a parasite. The common species, *Cystopus candidus*, attacks shepherd's purse (*Capsella Bursa-pastoris*) and, less frequently, some other closely related plants. It shows some specialisation in that its range of host plants is restricted. The part of the infected plant where the Fungus is most obvious is generally the inflorescence, the stem of which becomes blistered, enlarged, and distorted, and white on the surface.

The non-septate mycelium of the Fungus grows in the intercellular spaces of the host and bears numerous small rounded haustoria (Fig. 385, A), which penetrate the cells and function as absorbing organs. Shepherd's purse plants which are attacked by *Cystopus* are frequently also infected with another Fungus, *Peronospora*. Like *Cystopus*, this grows in the intercellular spaces of the host, producing haustoria on its mycelium. These haustoria are elongated and branched within the cells of the host and much larger than those of *Cystopus* (Fig. 386, A).

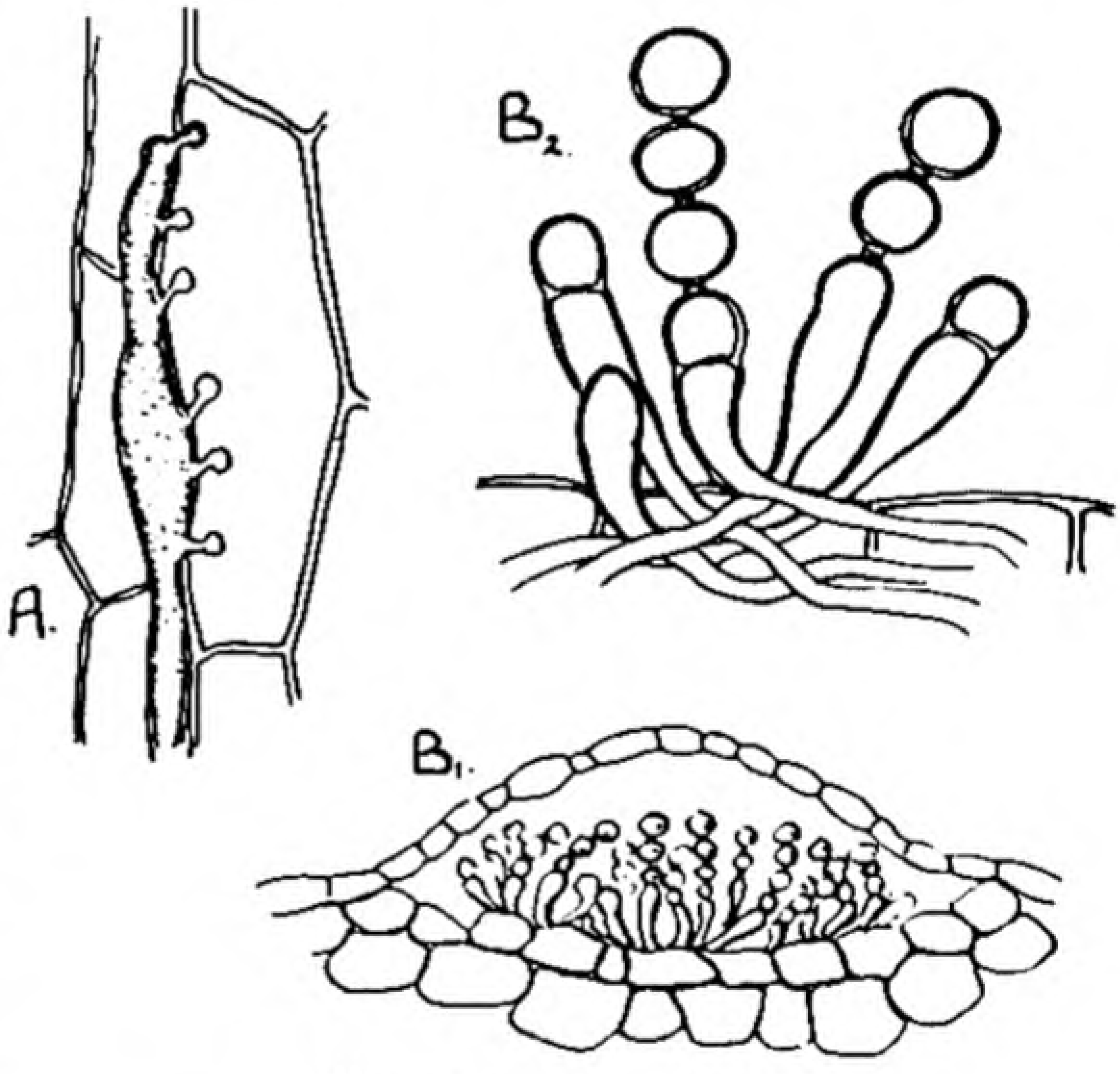

Fig. 385. *Cystopus*.
A, Filament of Mycelium with Haustoria;
B, Asexual reproduction;
(1) Low power; (2) High power.

19. Asexual Reproduction (Fig. 385, B)

Near the surface of the stem hyphae become branched and give rise, just beneath the epidermis, to a large number of closely-packed conidiophores. The ends of these hyphae are cut off by a septum and form multinucleate conidia. This process is repeated until each hypha bears a chain of conidia which press on the epidermis of the host, stretch it and, finally, rupture it.

Occasionally, as in *Pythium*, these conidia, after being shed, behave like zoosporangia and give rise to ciliated zoospores. If this development takes place on or near the surface of a suitable host, the hypha which results from the germination of the zoospore enters the tissue of the host and gives rise to a new mycelium. More usually the conidia germinate directly to give a hypha which enters a new host. Abundant production of these conidia permits a very rapid spread of the Fungus from plant to plant when conditions are suitable. The conidiophores of *Peronospora* are branched, each branch terminating in a single conidium which becomes abstricted (Fig. 386, B).

20. Sexual Reproduction

Sexual organs, oogonia and antheridia, are produced on hyphae present in the intercellular spaces of the parenchyma, e.g. of cortex and pith, of the host. The structure of the sexual organs and the details of the sexual process are similar to those of *Pythium de Baryanum*. The oospore develops a thick wall and is at first uninucleate, but its nucleus soon divides into numerous nuclei, involving meiosis. The oospores are freed only when the tissues of the host die and decay. On germination, after a period of rest, the oospore liberates a number of zoospores, each of which is capable of infecting a suitable host.

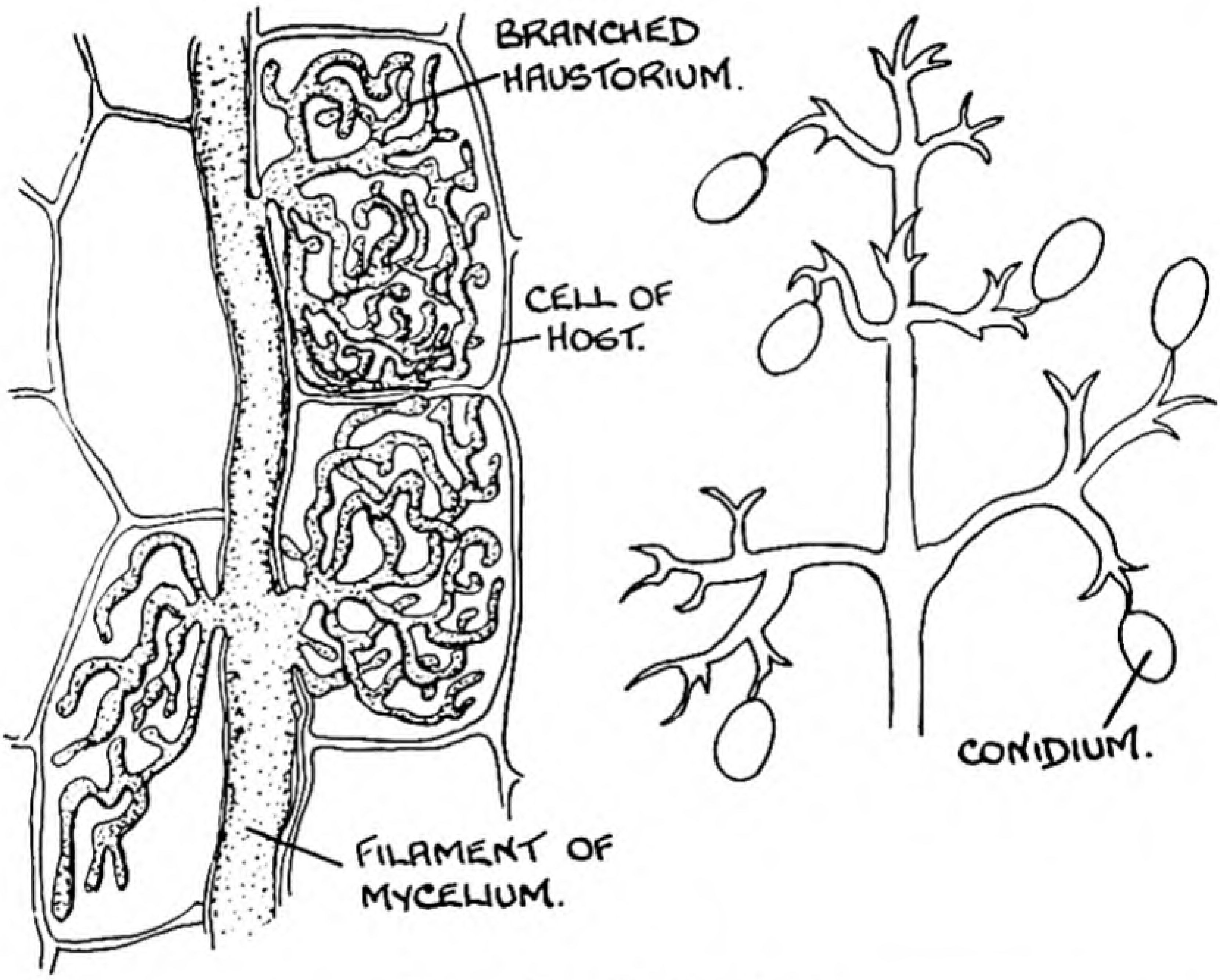

Fig. 386. *Peronospora*.
A, Filament of mycelium with haustoria; B, Asexual reproduction, conidiophore.

21. Response of Host Plant to Fungal Attack

We saw that the stem of the inflorescence of shepherd's purse when attacked by *Cystopus candidus* becomes more or less enlarged and distorted. This enlargement of the host organ represents a response by the host to the presence of the Fungus. The cells of the host are stimulated to grow in an abnormal way. With *Cystopus* this stimulation of the host is not very marked. Certain other parasitic Fungi, however, stimulate the cells of the host to rapid division and growth so that large galls or warts are produced. One of the Slime Fungi, *Plasmodiophora Brassicae*, sometimes present in the soil, attacks the roots of plants belonging to the genus *Brassica*, which includes many important crop plants. As a result of this attack the tissues of the root of the host plant, and more especially the cells of the medullary rays, are stimulated to divide and the root becomes extraordinarily deformed. So characteristic are these deformations that the plants attacked by *Plasmodiophora* and deformed in this way are said to be suffering from " club-root " or "finger and toe" disease. *Ustilago Treubii*, parasitising *Polygonum chinense* in Java, stimulates the cells of the host plant so that large galls are produced. *Puccinia caricis* (allied to *P. graminis*, see p. 500), which is found on *Urtica parviflora*, causes the production of hypertrophies (composed of host tissue) which are very rich in starch and may be used as food. Of a similar nature are many of the insect galls seen both on the roots and aerial parts of plants. Here the stimulation generally consists of the deposition of insect eggs within the tissue of the plant, and results in abnormal growth of the surrounding tissues, such that characteristic galls are produced.

PHYTOPHTHORA

22. Phytophthora Infestans

This phycomycetous Fungus is the cause of the common " blight " of potatoes. Another member of the genus causes a pink-rot of potato tubers. *P. Faberi* is a tropical species parasitic on cocoa, rubber (*Hevea*), etc. *P. Meadii* parasitises rubber, and *P. parasitica* may kill castor-oil seedlings. *Phytophthora infestans* has a life history similar in many ways to that of *Pythium* and *Cystopus*, but the sexual organs of this species of *Phytophthora* have not been observed to occur naturally, although they have been produced in artificial cultures of the Fungus. The non-septate mycelium of *P. infestans* ramifies in the leaves of the potato plant, where it is usually confined to the intercellular spaces. Cells adjacent to the hyphae die, so that small discoloured spots appear on the leaf. The spots enlarge and finally coalesce, so that the whole leaf dies and withers, or in wet weather, decays. Examination of infected leaves reveals, in addition to the intercellular mycelium, fungal hyphae projecting through the stomata on the lower side of the leaf. These hyphae branch repeatedly to form conidiophores and from the end of each branch a conidium is abstricted. The conidia are carried away by the wind, and each conidium usually functions as a zoosporangium. When it germinates it produces a number of motile zoospores. If these are formed on the surface of a potato leaf, each zoospore soon comes to rest and forms a hypha which enters the leaf either through a stoma or by piercing the cuticle and epidermis, and then grows within the leaf. Not only the leaves, but the stems and tubers of the potato plant are attacked by the Fungus, the mycelium of which winters in the dormant tubers. Other species of *Phytophthora* normally reproduce sexually as well as asexually and in general the sexual process resembles that of *Cystopus*. Branches of the fungal hyphae produce oogonia and antheridia. In each sexual organ, one of the many nuclei present becomes the nucleus of the non-motile gamete. Fusion of the gametes results in the production of an oospore and this, on germination, forms a very short mycelium which develops a branched conidiophore from which conidia are abstricted.

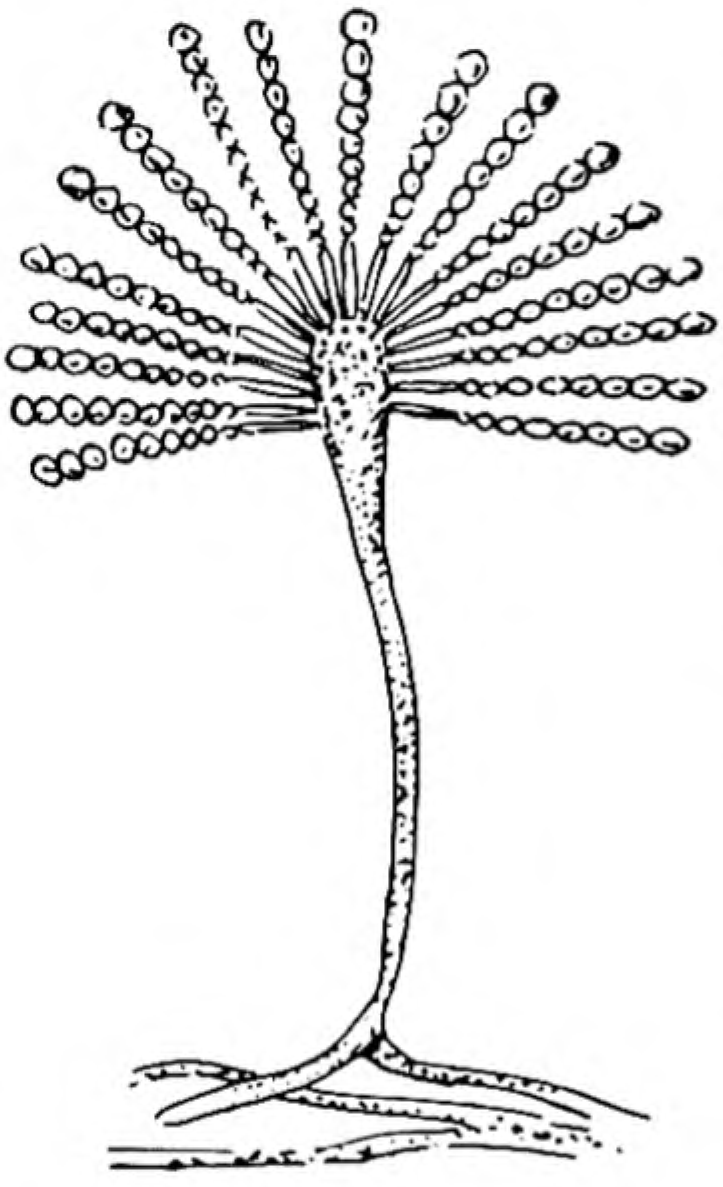

Fig. 387. *Eurotium.* Mycelium and Conidiophore in optical section.

EUROTIUM (ASPERGILLUS)

23. Habit and Structure

Eurotium is a saprophyte living on dead organic materials. It is frequently found on the surface of mouldy bread, damp fruit and vegetables, preserved fruit, etc., and belongs to the miscellaneous group of Fungi known as moulds, which form filamentous masses of mycelium on the substances on which they live. If a piece of dry, stale bread is kept under a bell-jar, *Eurotium*, a green mould, will probably appear on it, often in addition to *Mucor*. At first, before the reproductive bodies are developed, the mould is white; but when it enters on the reproductive stage it assumes a greenish colour.

The **mycelium** (Fig. 387) consists of a tangled mass of hyphae ramifying in and on the surface of the nutrient substratum. It is much branched, and the hyphae are divided at intervals by transverse septa. Each segment of a hypha contains a mass of granular vacuolated protoplasm, with several nuclei and oil-globules. The structure is coenocytic. Starch and plastids are absent. The hyphae which ramify beneath the surface absorb organic substances.

24. Asexual Reproduction (Fig. 387)

From the mycelium, numerous straight and, as a rule, non-septate branches grow up into the air. Each is given off from a hypha, usually at a point immediately behind a septum. These branches bear the **conidia**, and are therefore called **conidiophores.** The head of each conidiophore becomes spherical. On this spherical head arise a large number of peg-like outgrowths called **sterigmata,** into each of which pass several nuclei. From the apex of each sterigma as it elongates conidia are separated by abstriction one after the other, each with generally more than one nucleus. In this way rows or chains of conidia are formed on the sterigmata, the oldest conidia being at the apex of each row.

The conidia are small ovoid bodies with a greenish colour and more or less spiny surface. Their protoplasm contains several nuclei and oil-globules. The conidia are produced in enormous quantities, and are very readily carried through the air. It is because of their presence in the atmosphere that decaying substances so readily become infected with the Fungus. On reaching a suitable substratum they germinate to produce a new mycelium directly.

25. Sexual Reproduction (Fig. 388)

In *Eurotium* the same mycelium which has produced conidia also bears sexual organs. The female organ is called an **archicarp,** and the male an **antheridium.**

In the development of the archicarp the end of a hypha becomes coiled, at first loosely, but later very closely. It is septate and the segments are multinucleate. The apical segment is called the **trichogyne**: it is the receptive part of the female organ. The next segment is the **oogonium,** and is the female organ proper. The coiled septate part below the oogonium is the **stalk** of the archicarp.

Another hypha grows up from the mycelium near the archicarp, and arches over to the apex of the archicarp. It is septate and multinucleate. The terminal or apical segment is the **antheridium**; the lower septate part is the **stalk.** It should be noted that the protoplasm of the oogonium is not rounded off to form an oosphere. Fusion may take place between the antheridium and the trichogyne of the archicarp. The contents of the antheridium have not been observed to enter the oogonium. The fusion of male and female gametes has never been observed and probably does not occur. In some species of *Eurotium* it could not occur as the antheridium may never develop. The sexual process then is not completed normally. Instead, in some species at least, the nuclei in the oogonium appear to fuse in pairs. Sterile hyphae grow up from the stalks of the sexual organs and invest the oogonia. Whatever the preliminary stages have been, the oogonium next becomes septate, and from it small outgrowths, known as ascogenous hyphae, arise.

The ascogenous hyphae become septate and either the terminal or the penultimate cell of each forms an ascus which contains two nuclei (Fig. 389). It is probable that in most species of *Eurotium* the two nuclei in the ascus are derived from those originally in the oogonium, and which have not, up to this point, undergone any fusions. The two nuclei within the ascus now fuse. Meiosis occurs when the fusion nucleus divides to form eight nuclei, each of which becomes the nucleus of an ascospore. Each archicarp gives rise to a number of asci and these, together with their investment of sterile hyphae, form the fruiting body or perithecium. Later the innermost layers of sterile hyphae and the walls of the asci disorganise, and the spores lie free within the investing wall. They are set free when it decays and germinate under suitable conditions to form a new mycelium directly.

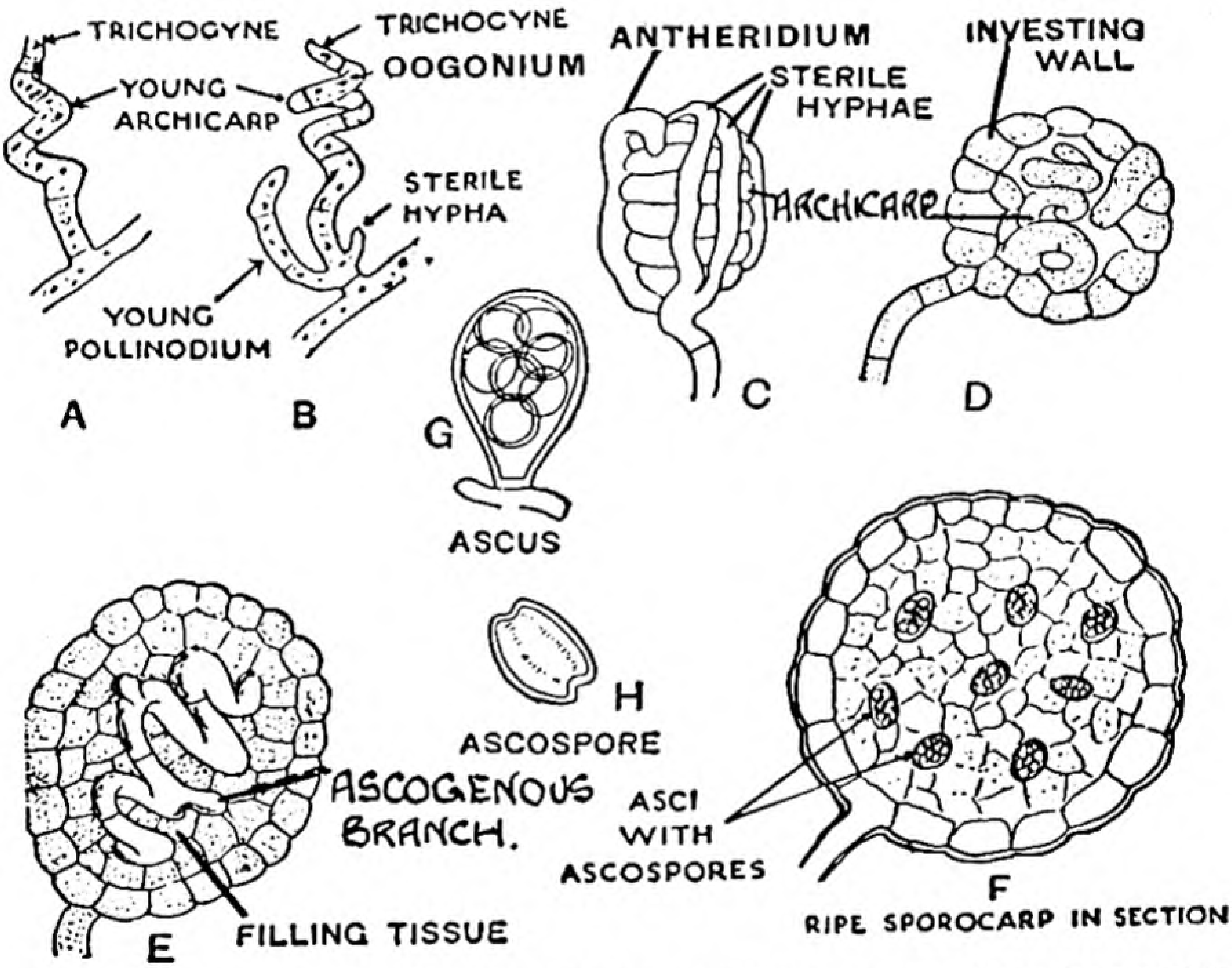
TRICHOGYNE
YOUNG ARCHICARP
TRICHOGYNE
OOGONIUM
STERILE HYPHA
YOUNG POLLINODIUM
A
B
ANTHERIDIUM
STERILE HYPHAE
ARCHICARP
C
INVESTING WALL
D
G
ASCUS
H
ASCOSPORE
ASCOGENOUS BRANCH.
FILLING TISSUE
E
ASCI WITH ASCOSPORES
F
RIPE SPOROCARP IN SECTION

Fig. 388. *Eurotium*. DEVELOPMENT OF PERITHECIUM AND ASCOSPORES.

26. Taxonomic Position, and Cytology of the Ascus

Eurotium is one of the large group of Fungi called the Ascomycetes which are characterised by the production of ascospores within an ascus. In many Ascomycetes fusion of male and female gametes (*i.e.* fertilisation) is a necessary prelude to ascus formation. Two nuclei are usually present in the young ascus. These nuclei are presumably haploid. They fuse, and the fusion nucleus is diploid. During the three successive nuclear divisions that take place in the ascus, meiosis occurs, so that the nuclei of the eight ascospores are haploid. These ascospores give rise to a mycelium with haploid nuclei.

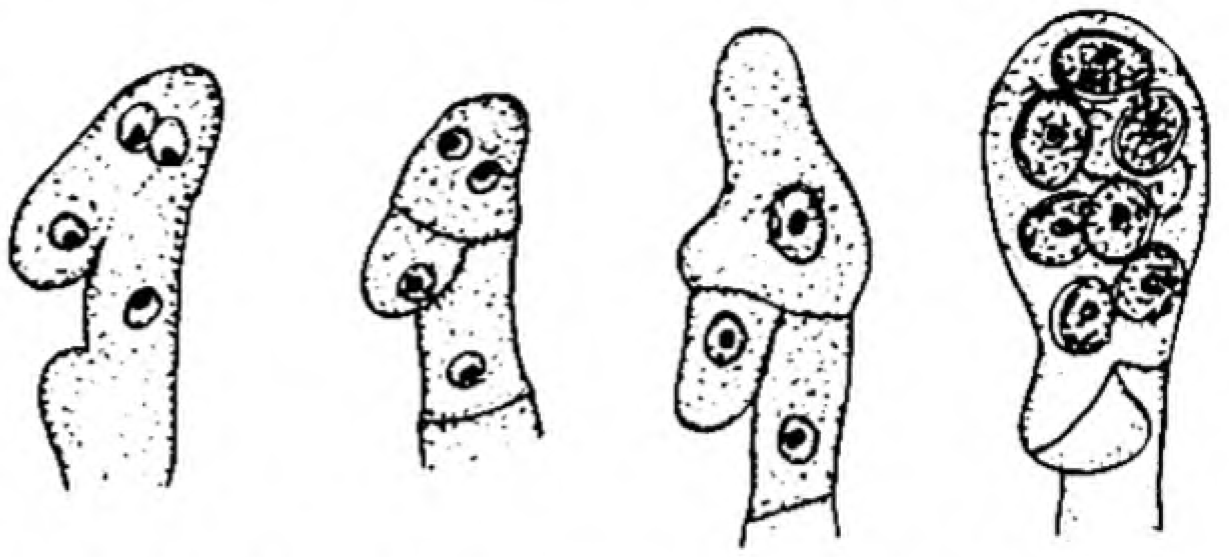

Fig. 389. *Eurotium*, CYTOLOGY OF ASCUS.

27. Penicillium glaucum

This is a blue mould very similar in habit and structure to *Eurotium*. The apex of each conidiophore, instead of being globular, divides into a number of finger-like processes bearing the sterigmata (Fig. 390). The conidia of this Fungus, if grown in a sugar solution, under certain conditions, give rise, not to a filamentous mycelium, but to isolated cells resembling yeast. This is the **torula condition** (cf. *Mucor*, p. 480). Like yeast, it induces fermentation.

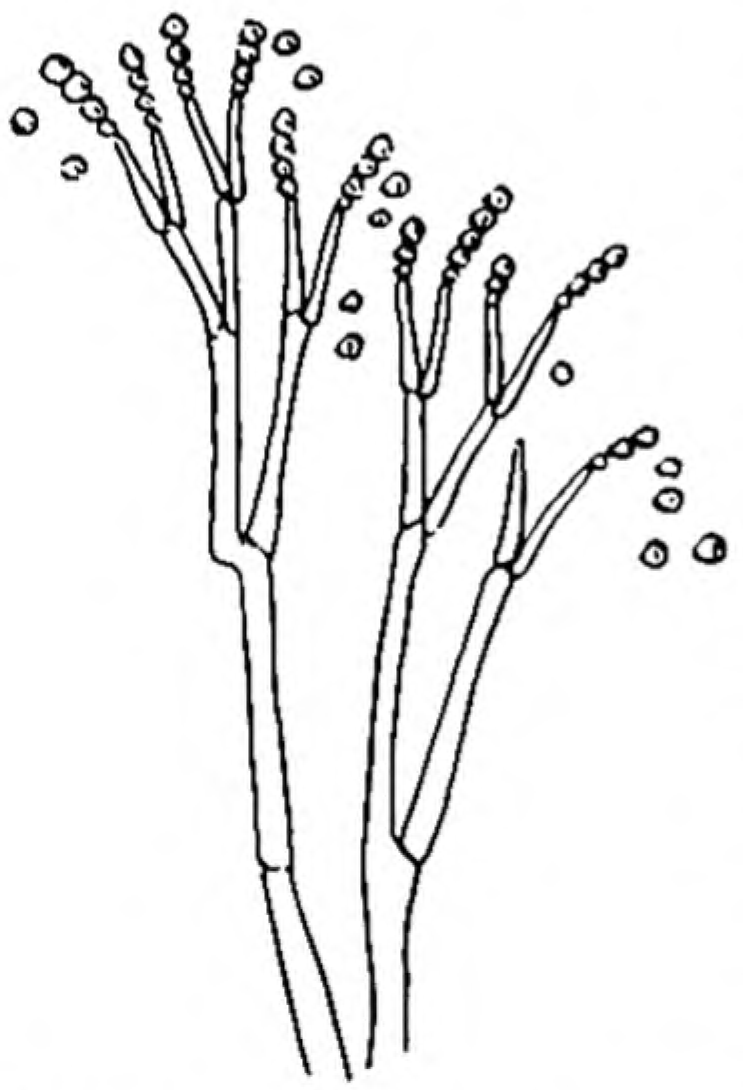

Fig. 390. *Penicillium*, CONIDIOPHORE AND CONIDIA.

ERYSIPHE

28. Erysiphe

Erysiphe is another genus of Fungi belonging to the Ascomycetes. The members of the genus are parasites and are popularly known as white or powdery mildews. Erysiphe is parasitic on the aerial parts of some herbaceous plants. On the parasitised plants there is an abundant development of superficial mycelium consisting of uninucleate cells. This mycelium forms a white, powdery covering over the leaf or stem, and the hyphae penetrate the epidermal cells only, by means of their haustoria. Many crop-plants are attacked by various species of *Erysiphe*. *E. graminis* is the cause of mildew of cereals and grasses, whilst *E. polygoni* causes mildew of peas and swedes.

29. Asexual Reproduction

From the superficial mycelium upright, unbranched septate conidiophores are developed. From the ends of these conidiophores large ovoid conidia are cut off by successive cell divisions.

In this way a chain of conidia is formed at the end of each conidiophore (Fig. 391, A). These conidia are readily distributed by the wind, and if they alight on a suitable host they germinate to give a fresh mycelium. The rapid spread of the Fungus during the summer is effected by means of these conidia.

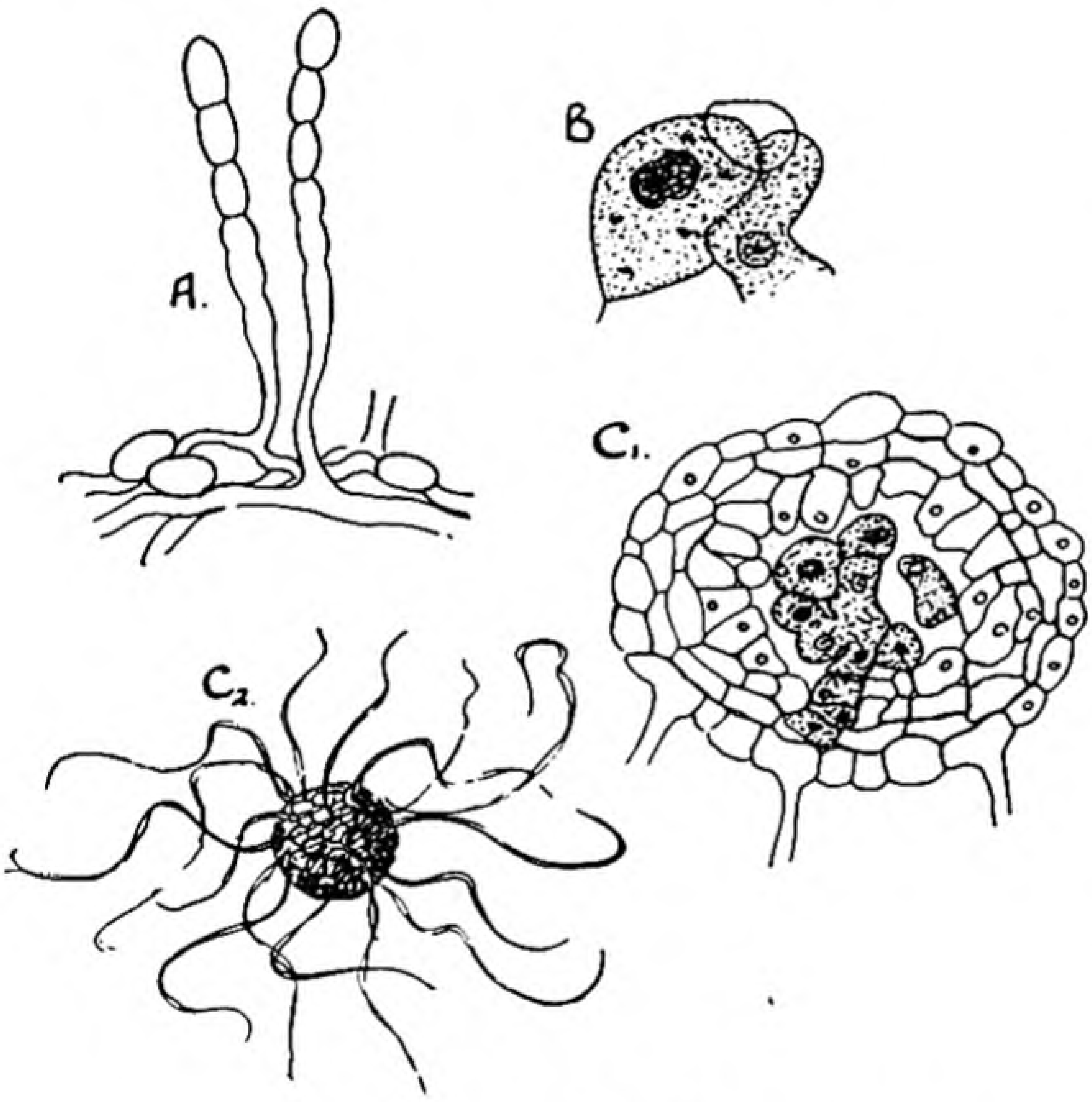

Fig. 391. *Erysiphe.*

A, Asexual; B, Sexual organs; C, Perithecium, (1) Section, young stage; (2) External, mature.

30. Sexual Reproduction

This has been described for *Erysiphe polygoni*, which occurs on the shoots of various hosts. The mycelium growing over the surface of the host sends up short, erect lateral branches in pairs, which develop into the sexual organs. The oogonium is slightly swollen and uninucleate. The antheridium is cut off from the tip of a slender filament arising near the base of the oogonium. It tends to hook over the oogonium at its apex, and is also uninucleate (Fig. 391, B). The separating walls between antheridium and oogonium break down, and the nucleus of the former enters the oogonium and fuses with its nucleus. The oogonium now elongates and divides by transverse septa to form a row of cells. The penultimate cell of this row usually contains several nuclei. From it numerous ascogenous hyphae bud out and branch, and the ends of the branches give rise to asci. Each ascus usually contains eight ascospores. Meanwhile, sterile hyphae have been developing and investing the sexual organs. The outer ones harden and form the protective covering to the mature fruiting body or perithecium; the inner ones serve as nutritive material to the developing asci. In addition, characteristic filamentous perithecial appendages develop and branch irregularly. These serve to anchor the perithecium to the substratum (leaf or stem) on which it forms (Fig. 391, C). The ascospores are usually set free by the decay of the wall of the perithecium in the spring. They are scattered by the wind, and those which find a suitable host germinate, giving rise to a new mycelium.

Some doubt has been cast on the occurrence of fertilisation both in *Erysiphe* and in some of the related genera. The antheridium appears to be non-functional, and the asci develop apogamously. In either case, the young ascus has two nuclei which fuse, and the fusion nucleus divides to give the nuclei of the eight ascospores. During this process meiosis occurs, and the ascospores are haploid.

CLAVICEPS PURPUREA (ERGOT OF RYE, ETC.)

31. General Life History

The life history of this Fungus shows three well-marked stages, and affords an illustration of the polymorphism which is so common amongst Fungi.

(1) The **Sphacelia** or "**Honey-dew**" **stage** is found on various cereals and grasses. It has been most carefully studied in the case of rye (*Secale cereale*), but it also occurs on barley, wheat, etc., and on some of the grasses commonly found on roadsides, in meadows and in waste places (e.g. *Lolium perenne*). It is the active parasitic stage in which the Fungus attacks the developing ovary and forms a mycelium which grows vigorously in the ovary and reproduces itself by means of conidia (Fig. 392).

(2) The **Sclerotium stage** is the resting or winter stage. In autumn the mycelium enclosed in the ovary wall forms a hard, slightly curved body, of a dark purple or black colour, which protrudes from between the paleae of the flower, and may attain the length of about an inch (Fig. 394, A). It falls to the ground and undergoes no change till the following spring. It was to this body that the name ergot was first given. Hard resting bodies of this kind are formed by many Fungi and are called **sclerotia.**

(3) The **Ascospore stage.** The sclerotium or ergot eventually produces a number of club-headed structures, called **stromata** (Fig. 394, B), in which asci and ascospores are developed. From these the Sphacelia stage again arises.

At first the connexion between these three stages was not recognised. They were regarded as distinct Fungi and received the generic names *Sphacelia, Sclerotium,* and *Claviceps* respectively. The last is now taken as the generic name of the Fungus in all its forms.

32. The Sphacelia Stage (Figs. 392 and 393)

The ascospores, which are peculiar in being very slender and thread-like (Fig. 396 B), are liberated just when the flowers of the host plants are appearing. They are carried to the flowers by wind and there germinate. In the process of germination swellings appear on the ascospore, and at these points the germ-tubes are developed. They pierce the epidermis and make their way into the tissue, through which they ultimately reach the base of a young ovary.

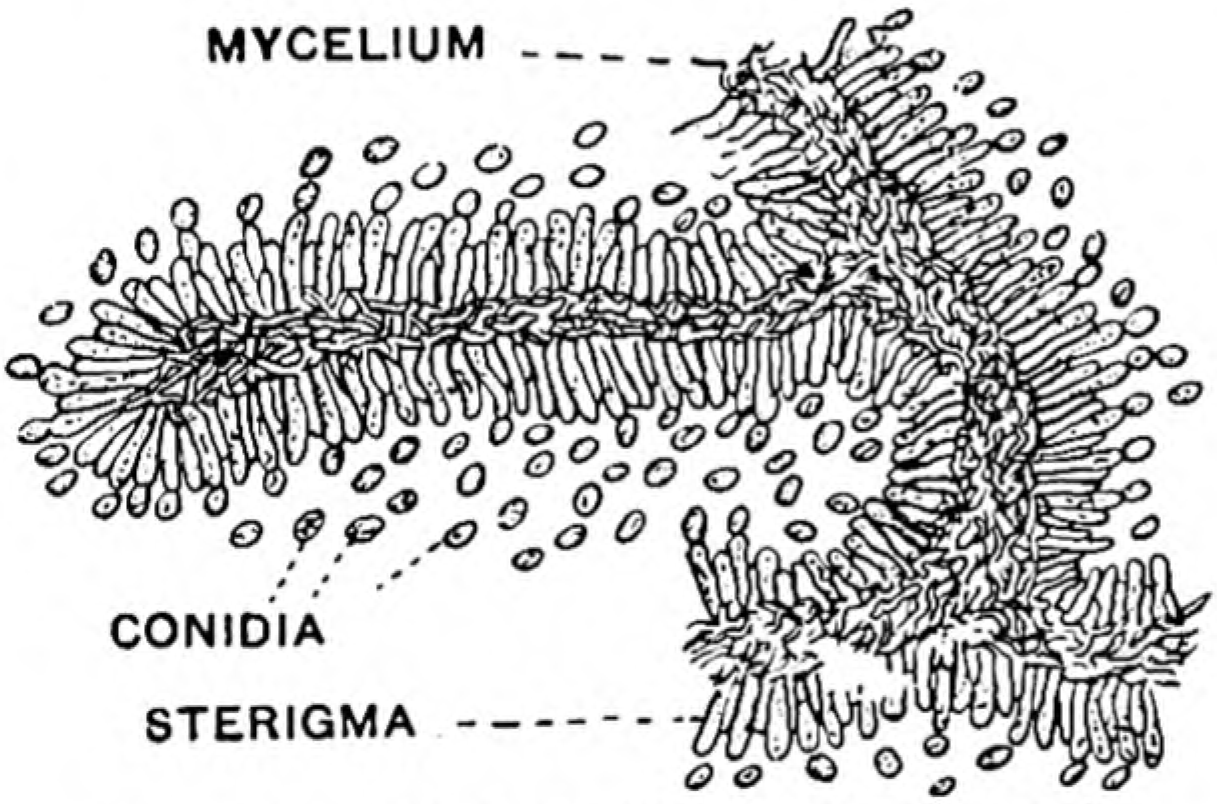

Fig. 392. *Claviceps* (SPHACELIA STAGE). Section of Conidiophore.

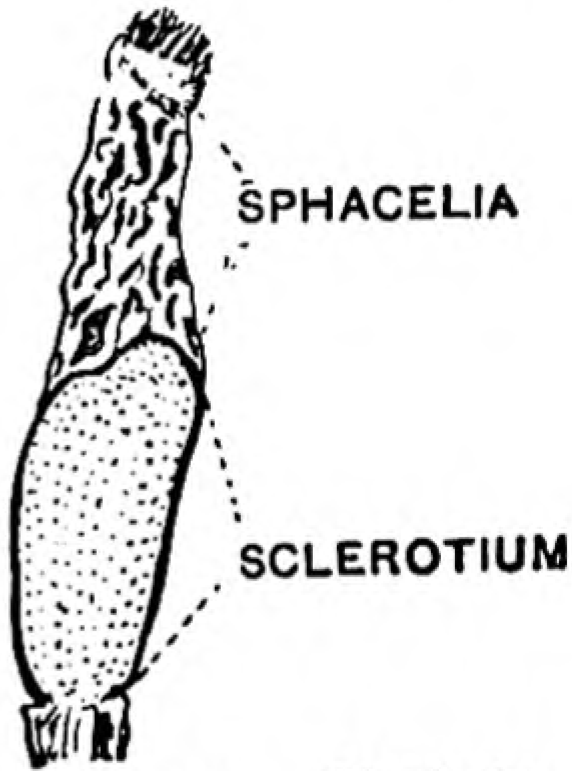

Fig. 393. *Claviceps.* Vertical section through developing sclerotium.

The **mycelium** which is rapidly developed consists of septate hyphae. It not only ramifies in the tissue of the ovary, but also, after a time, spreads over its surface and envelops the greater part of it with a dense white covering of interwoven hyphae, showing numerous folds and convolutions. This investment is the **conidiophore.** The free ends of the hyphae become slightly swollen, and form **sterigmata** from which small oval **conidia** are successively abstricted (Fig. 392).

The conidia are developed in great numbers, and are embedded in a sweet and somewhat viscid fluid which is formed by the disorganisation of the outer layers of the walls of both hyphae and conidia. This fluid is called "**honey-dew.**" Flies and other insects are attracted to it, and by their agency the conidia are carried to other plants. A conidium carried in this way to another flower sends out a germ-tube which pierces the base of the ovary and produces another mycelium.

33. The Sclerotium Stage (Fig. 393)

When the growth of the mycelium has continued for a considerable time, the mass of interwoven hyphae in the ovary becomes compact, and forms a false tissue which is the beginning of the sclerotium. The outer layers of this tissue become dark-coloured and growth now goes on actively in this region. The sclerotium rapidly elongates and assumes a curved horn-like shape.

The sclerotium or ergot is fully formed just when the grain ripens. It then protrudes from between the paleae, but is easily detached. Unless the crop is harvested early, it falls to the ground and there remains in a dormant condition till the following spring (Fig. 394, A).

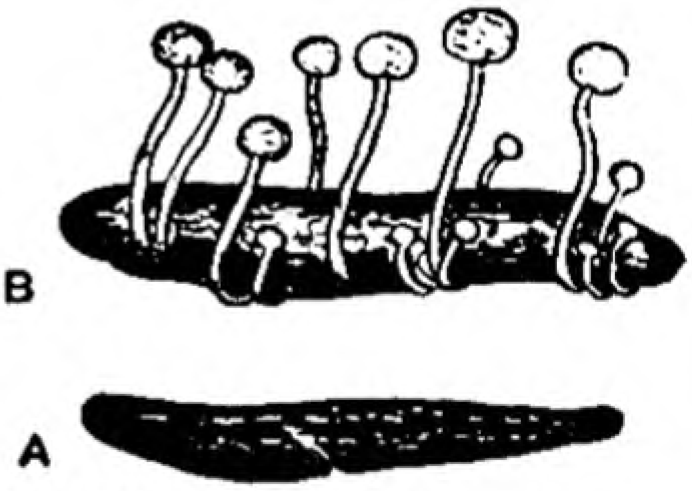

Fig. 394. *Claviceps.*

A, Sclerotium, resting stage; B, Sclerotium with stromata.

If a transverse section of the sclerotium is taken, it is found to consist of a dense pseudoparenchyma formed of fine united hyphae. The outline of the section is somewhat irregular and is interrupted in places by fissures or cracks. The outer layers are very dark-coloured.

The sclerotia are rich in oil and contain a number of alkaloids. The value of the sclerotium or ergot as a drug depends on its content of alkaloids. Some of these alkaloids are able to stimulate plain muscle, especially of the uterus, and for this reason ergot is widely used in midwifery to assist delivery in labour and to control uterine haemorrhage. If grain containing ergot is used for bread making serious disease may be caused amongst the persons who consume the bread. Gangrene of the extremities may arise from this cause.

34. The Ascospore Stage

In spring or early summer the sclerotia begin to develop their stromata. The first sign of development is the appearance of a number of swellings on the surface and sides of the sclerotium. Then the dark-coloured outer layer is gradually ruptured, and the light-coloured heads of the stromata protrude. The development of each stroma is due to the outgrowth of a tuft of hyphae from the lighter-coloured inner tissue of the sclerotium.

Each stroma consists, when fully developed, of a purplish stalk, an inch or more in length, and a rounded head of a light brown or orange colour (Fig. 394, B). As in the case of the sclerotium, the hyphae of the stroma are closely interwoven and united, and form a false tissue. The head is covered with minute papillae, on which are situated the openings or **ostioles** of numerous flask-shaped cavities, called **perithecia,** which lie in the peripheral tissue of the head. These perithecia can be readily seen in a vertical section of a stroma (Fig. 395).

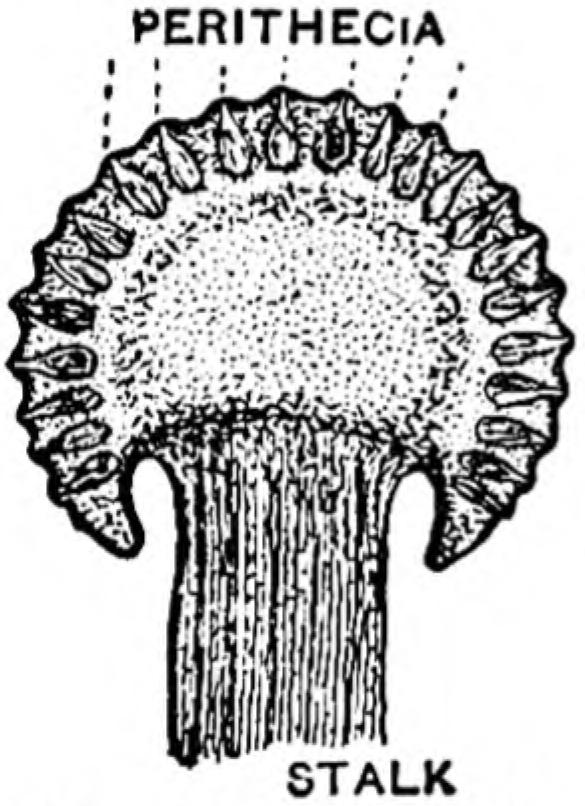

Fig. 395. *Claviceps.*
Vertical section through a stroma, showing the perithecia.

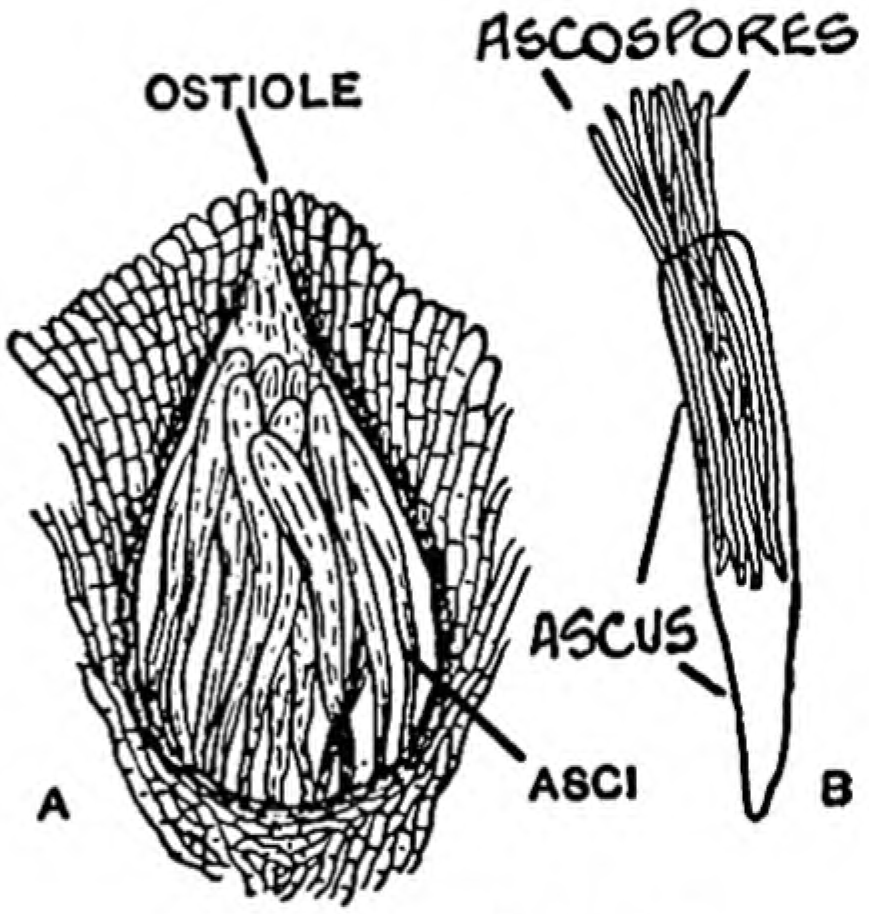

Fig. 396. *Claviceps.*
A, Section through a perithecium, showing the asci; B, a single ascus, ascospores escaping.

From the cells in the floor of each perithecium are developed a number of elongated club-shaped **asci,** which project upwards towards the ostiole (Fig. 396, A). The contents of each ascus divide to form from six to eight thread-like **ascospores** (Fig. 396, B). When the asci are ripe they burst. The ascospores escape through the ostioles, and some of them, carried as already described to the young flowers of a grass, produce the *Sphacelia* stage again.

During the formation of the perithecia sexual organs—antheridia and oogonia—arise, but they appear to abort and the asci are derived from ordinary cells of the mycelium.

35. Notes on the Life History

Like *Eurotium*, *Penicillium* and *Erysiphe*, *Claviceps* belongs to the Ascomycetes. It is, however, placed in a different division of that group, as the ascocarp or perithecium is not a closed structure as in *Eurotium*, but is flask-shaped, and has a distinct opening, the **ostiole.**

The life history of *Claviceps* is more complicated than that of *Eurotium*, owing to polymorphism. The mycelium of *Eurotium* after a period of asexual reproduction by conidia, produces sexual organs as a prelude to ascus formation. In *Claviceps* the sexual organs degenerate, and ascocarps or perithecia are produced apogamously. A graphical representation of the life history is given in Fig. 397.

The abundant production of conidia permits the rapid spread of the Fungus throughout the flowering period of the host plant, whilst the resting and resistant sclerotia provide a means by which the Fungus can overwinter.

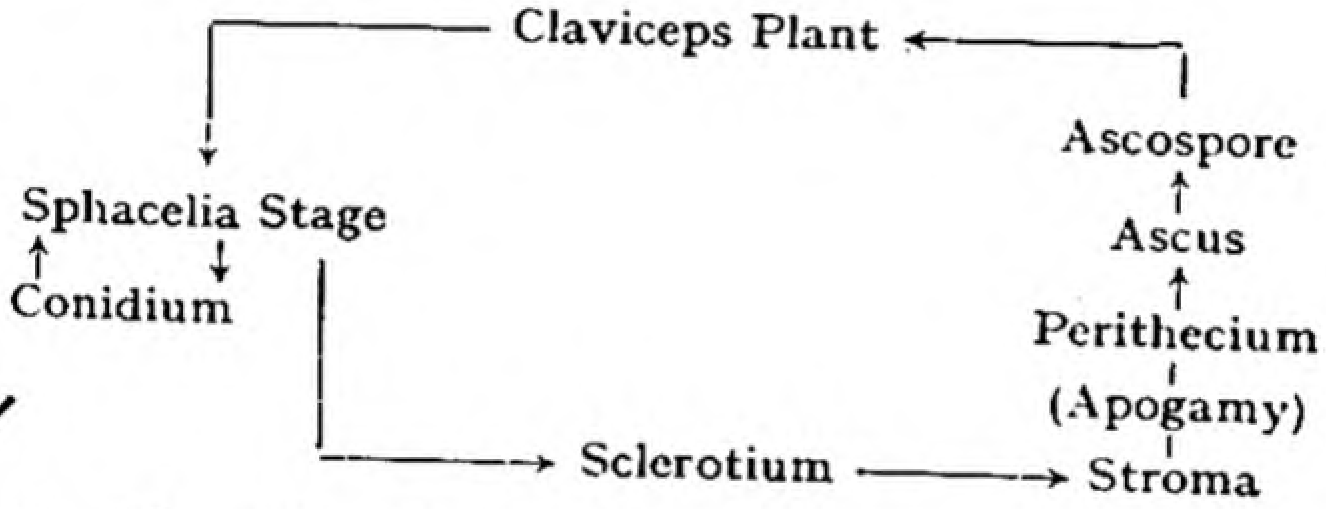

Fig. 397. *Claviceps.* GRAPHICAL REPRESENTATION OF LIFE HISTORY.

36. Cytology of Ascus Formation

The steps leading to ascus formation differ considerably in different members of the Ascomycetes. Commonly, sexual organs are produced but they do not always function. Of the forms described *Eurotium* and *Claviceps* have no proved functional sex organs, and even in the Erysiphales, although some observers claim that the antheridium is functional, and behaves as described for *Erysiphe polygoni*, others claim that the only proved nuclear fusion is that in the young ascus. If this is so, the fusion nucleus is diploid and after meiosis eight haploid ascospores are formed.

But in some cases, notably among the Discomycetes, not included among our types, but characterised by a flat, open fructification bearing asci on the surface, functional sexual organs do exist. Here there is a passage of a male nucleus into the oogonium and a fusion of male and female nuclei there. This nuclear fusion is followed by another fusion of two nuclei in the young ascus. These two fusions result in the nucleus of the young ascus being tetraploid (*i.e.* having four haploid sets of chromosomes), and in the three nuclear divisions which give rise to the eight ascospores the chromosome number is twice reduced. Hence all the spores are once more haploid and give rise to a haploid mycelium. This double reduction within the ascus is known as brachymeiosis, but the student is warned that mycologists are by no means unanimous as to its existence.

SACCHAROMYCES (= YEAST)

37. Habit and Structure

This is the Fungus which usually brings about alcoholic fermentation in sugar solutions. *S. cerevisiae* is the beer-yeast (brewer's yeast); *S. ellipsoideus* sets up fermentation in grape-juice in the manufacture of wine. The yeast-plant is a saprophyte, and grows most actively in solutions containing, in addition to sugar, small quantities of nitrogen compounds.

The **mycelium** is not, as in most of the other Fungi, a branched filamentous structure, but consists of isolated cells or groups of cells (Fig. 398). Each cell is more or less ellipsoidal. Within the delicate membrane is granular protoplasm surrounding a relatively large vacuole. The nucleus lies to the side of the vacuole. It has a relatively small amount of chromatin and a normal nucleolus. In the cytoplasm are oil globules and granules of glycogen and volutin.

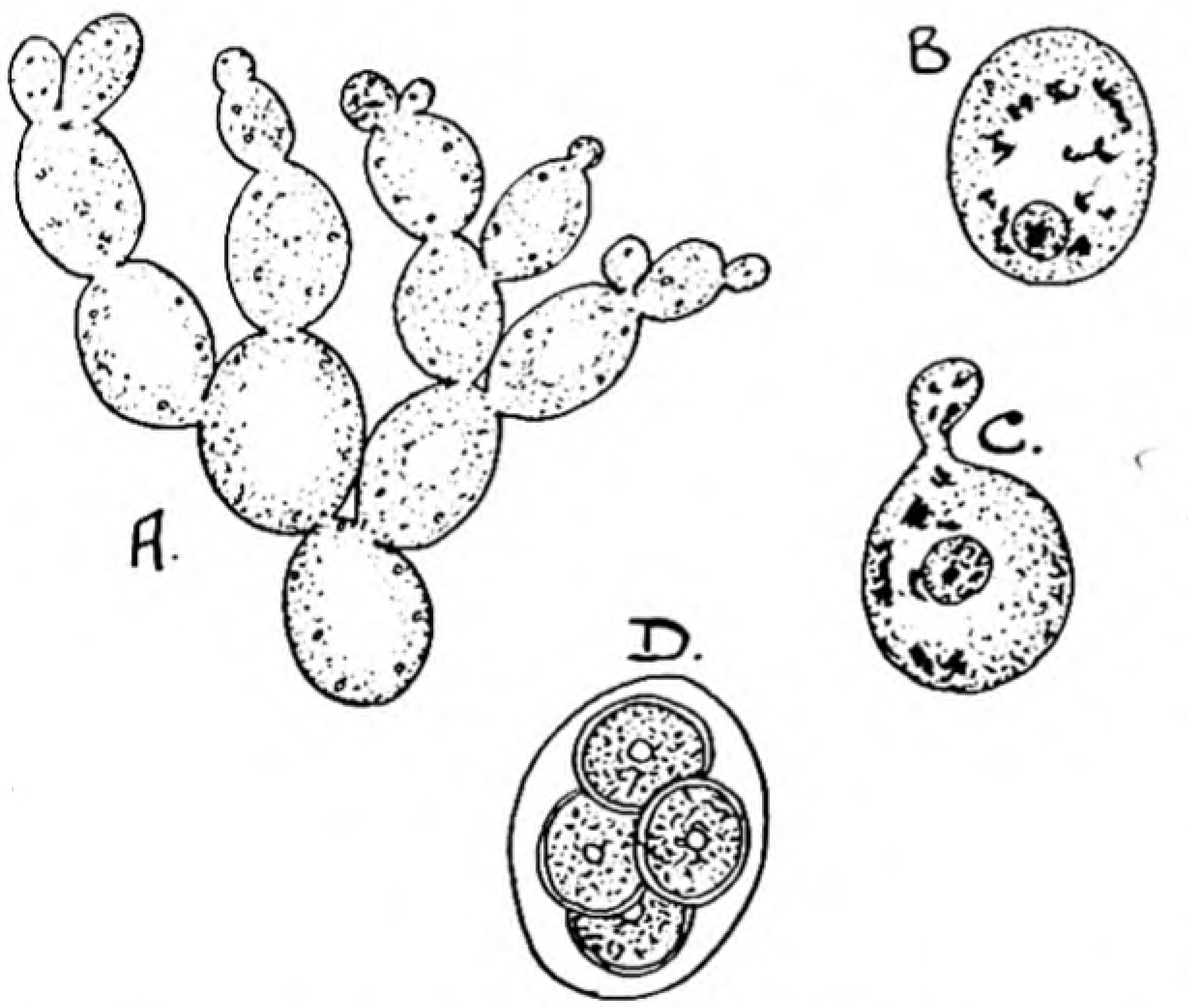

Fig. 398. *Saccharomyces.*
A, Yeast plant; B, Cell; C, Budding; D, Containing 4 ascospores.

38. Vegetative Reproduction

The common method of reproduction is by vegetative budding. If yeast in an active state of growth is examined, it is found that many of the cells give rise to a small outgrowth which gradually increases in size and finally becomes a separate yeast-cell. This process is known as **budding.** Each bud at maturity has the same structure as the parent cell, and may repeat the process of budding. In this way colonies of yeast-cells may be built up.

The individual cells may be separated, especially if the medium is disturbed.

39. Spore Reproduction

This occurs naturally under conditions unfavourable to active vegetative growth, and can be induced in artificial culture media. The individual yeast-cell becomes a sporangium and its nucleus divides into two, four or eight. Each nucleus aggregates around it some of the cyloplasm of the parent cell, and becomes surrounded by a resistant cell-wall, forming a resting spore. One, two, four or eight such spores are therefore present in each sporangium and are liberated by the breaking down of the sporangium wall. These spores are regarded as ascospores, and the sporangium (cell) in which they arise as an ascus. Accordingly, *Saccharomyces* is placed in the Ascomycetes.

As in the other Ascomycetes, the ascospores of *Saccharomyces* are found to be haploid. They germinate under suitable conditions, but their behaviour varies. Several strains of yeast have recently been studied in detail and it has been found that a process of fertilisation, resulting in zygote formation, takes place. There appears to be no established system governing zygote formation; two spores may unite either before or after germinating, or a spore may unite with a haploid vegetative cell, or two haploid vegetative cells may conjugate. The zygote is presumably diploid and, by budding, gives rise to a colony of diploid cells. These cells are ellipsoidal and much larger than the more spheroidal cells which may be produced from an ascospore to form a haploid colony. It appears, therefore, that fertilisation results in cells of increased size and capacity for growth. Eventually cells from these diploid colonies produce ascospores after meiosis. The life history of *Saccharomyces* can be rendered graphically:—

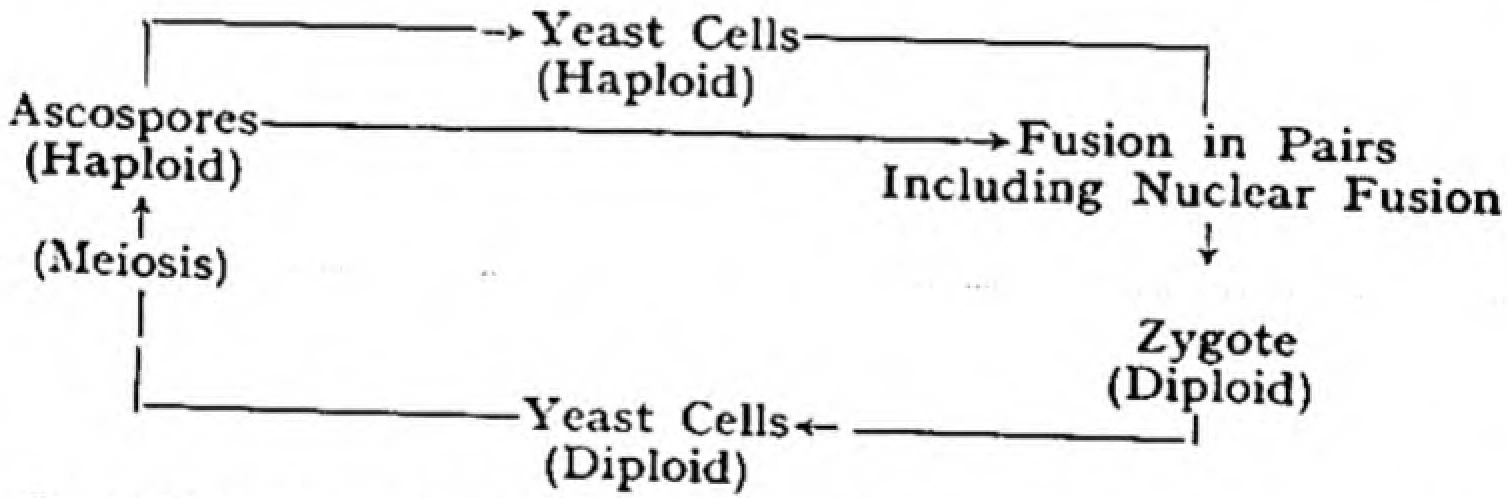

Fig. 399. LIFE HISTORY OF *Saccharomyces*, GRAPHICALLY REPRESENTED.

40. Alcoholic Fermentation

Alcoholic fermentation is the name given to the process in which various sugars are broken down to form alcohol and carbon dioxide. Alcoholic fermentation results from the metabolic activities of yeast and proceeds actively in sugar solutions inoculated with yeast. The process may be summarised by the chemical equation

$$C_6H_{12}O_6 \longrightarrow 2C_2H_5OH + 2CO_2 + 25 \text{ Cals.}$$

Not all the sugar decomposed can be accounted for by this reaction. Besides ethyl alcohol, which is the main product of the fermentation, small quantities of higher alcohols, glycerol and succinic acid are produced. The fermentation goes on both in the presence and absence of oxygen, but appreciable growth of the yeast occurs only when oxygen is present. Under these conditions some of the sugar is utilised by the yeast in the processes of growth and some may be completely oxidised to carbon dioxide and water. Hence less alcohol is produced per unit weight of yeast in the presence of oxygen than in its absence. Living yeast is not essential to the fermentation. A dead yeast preparation, in which the enzymes of the yeast are present, is effective in promoting fermentation, clear evidence that fermentation is an enzyme-controlled process. The enzyme or rather the whole complex of enzymes responsible for the process are collectively called zymase. The sugars glucose and fructose can be fermented directly. Sucrose cannot be fermented until it has been converted into glucose and fructose. Since yeast-cells produce the enzyme invertase which brings about the hydrolysis of sucrose to fructose and glucose, the yeast is able first to hydrolyse the sucrose and then to ferment the product of this hydrolysis. Complete oxidation of a gram-molecule of glucose results in the liberation of 673 Cals. of energy. Fermentation of an equal amount of glucose liberates only 25 Cals. of energy. As an energy-producing process therefore fermentation is extremely wasteful of sugar. In spite of its inefficiency the fermentation process is the method by which the yeast plants obtain some of their energy.

When sugar solutions are fermented by yeast the fermentation ceases when the concentration of alcohol reaches about fifteen per cent., owing to poisoning of the yeast-cells. Alcoholic liquid containing a greater amount of alcohol than this cannot be produced by fermentation.

Alcoholic beverages produced by fermentation of sugar solutions are legion. Sometimes, as in wines, the sugar (of the grape) is fermented directly. In other cases starch-containing seeds (grains) are allowed to begin germination so that the starch they contain is converted by the action of diastase to maltose and glucose. Yeast then converts these sugars to alcohol and carbon dioxide. Beer and ales are produced in this way. Spirits containing a higher proportion of alcohol are produced by the distillation of fermented sugar solutions.

The process of fermentation has been expressed by a chemical equation identical with that used to express the process of anaerobic respiration. The zymase complex of enzymes produced in yeast-cells and capable of inducing fermentation is known to be widely distributed in other plant tissues, and many botanists believe that fermentation is in fact a process identical with anaerobic respiration.

PUCCINIA

41. General

Puccinia is a large genus, all the members of which are parasitic, and belongs to the large group of Fungi, the Basidiomycetes. These are characterised by the production at some stage of their life history of exogenous basidiospores on a characteristic structure, the basidium. The different species of *Puccinia* parasitise various plants and are the cause of many rust diseases. *Puccinia malvacearum* is hollyhock rust. *P. graminis* is the cause of black rust of wheat. It parasitises barberry and wheat and spends part of its life history on each of the two hosts.

PUCCINIA GRAMINIS

42. Spermogonia and Aecidia

In the spring, on the leaves of barberry attacked by the Fungus, numerous small red dots appear on the upper surface. These dots are at first yellow, then brown in colour, due to the formation of **spermogonia,** whilst on the lower side of the leaf orange-coloured pustules (aecidia or cluster-cups) make their appearance. Within the leaf is the branched, septate mycelium of the Fungus growing in the intercellular spaces. The mycelium gives rise to small haustoria which penetrate the cells and function as absorbing organs. Hyphae of the Fungus become localised at the point where a spermogonium will appear, turn upwards and lie more or less parallel, finally converging to a point and rupturing the upper epidermis of the leaf. The spermogonium therefore consists of a flask-shaped cavity in the leaf (Fig. 400, A) with a wall of tightly-packed fungal hyphae and an opening to the exterior—the ostiole.

From the sides and base of the spermogonium grow two kinds of hyphae. Some are very long and delicate and protrude from the ostiole. They are *receptive hyphae*. Others give rise to small, uninucleate *spermatia*, which are abstricted and extruded from the ostiole in a drop of mucilage. This attracts insects and by their agency the spermatia are transferred from one spermogonium to another. It has been shown that two types of spermogonium exist, of opposite strain, so that in any one spermogonium all the receptive hyphae and all the spermatia are of the same strain, either + or −. By insect agency, + spermatia from a + spermogonium will be transferred to − receptive hyphae of a − spermogonium and vice versa. It has been suggested that when this happens the separating walls break down and the nucleus of the spermatium enters the receptive hypha, travels down it and comes to rest in a uninucleate cell at its base. This cell now contains two nuclei. From all such binucleate cells in the barberry leaf, fungal hyphae develop and become septate, each cell containing two nuclei. These hyphae with binucleate cells eventually aggregate to form the **aecidia,** embedded in the mesophyll of the barberry leaf (Fig. 400, B). Each aecidium consists of a wall of compact hyphae enclosing a cavity into which grow other hyphae having binucleate cells. The aecidium enlarges, and finally ruptures the epidermis of the leaf. The last mentioned hyphae function as conidiophores; each cuts off a chain of cells in which every alternate cell becomes a binucleate **aecidiospore,** whilst the intervening cells remain small and on drying permit the aecidiospores to separate readily and be dispersed by air currents.

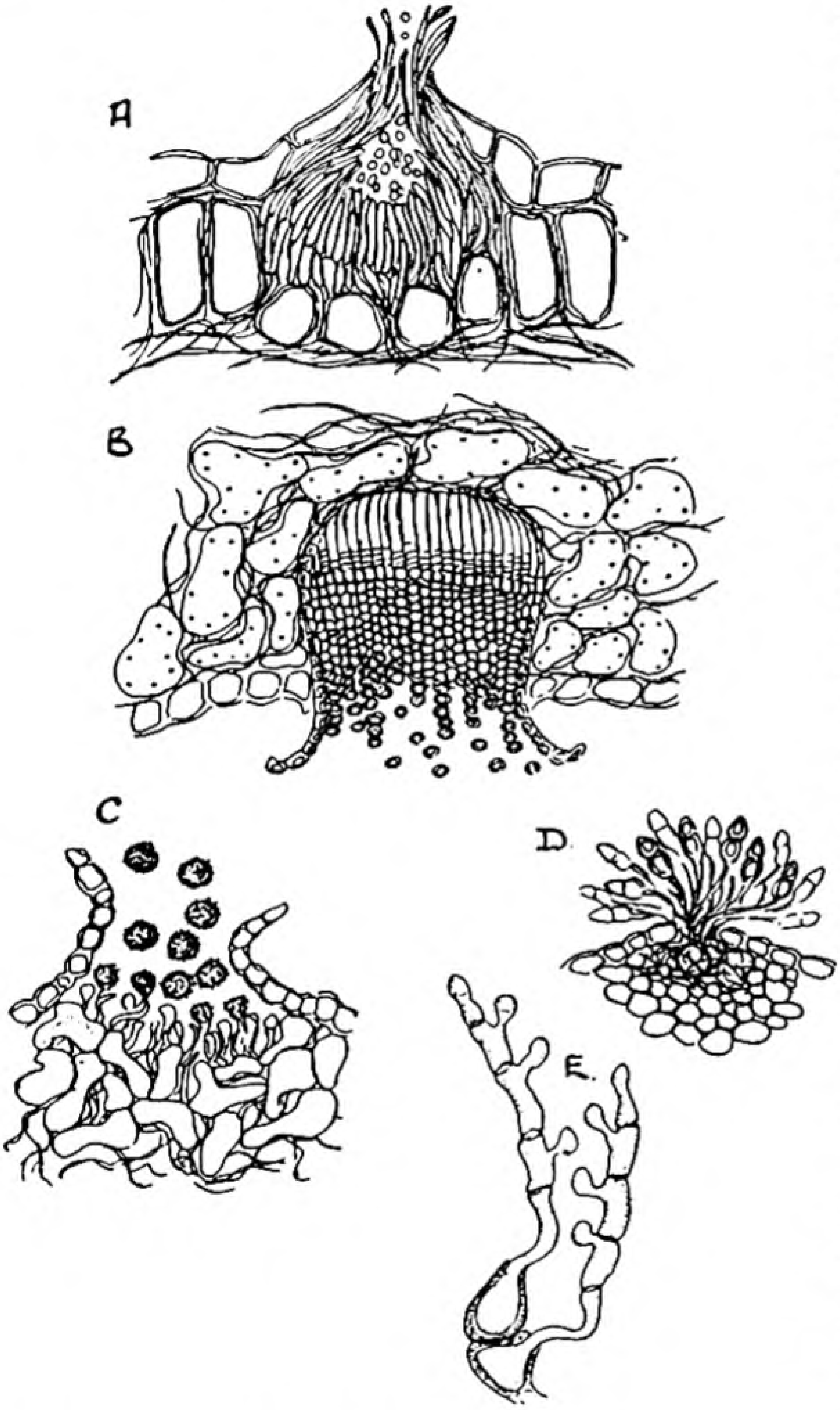

Fig. 400. *Puccinia.*

A, Spermagonium, section; B, Aecidium, section; C, Uredospores, section; D, Teleutospores, section; E, Teleutospore germinated—Basidia.

43. Uredospores

If an aecidiospore comes to rest on a leaf of wheat it germinates, giving rise to a slender hypha which enters the leaf through a stoma. Inside the leaf the hypha ramifies in the intercellular spaces of the mesophyll and produces an extensive mycelium. The hyphae are septate and each cell is binucleate. Ultimately the epidermis of the leaf is broken by longitudinally elongated scars, exposing erect hyphae, each of which is terminated by a binucleate **uredospore.** When ripe the uredospores are yellowish-brown, giving their colour to the lines along which the epidermis is split. These lines are called **uredosori.** Each uredospore is protected by a thick wall which has, however, thin spots or germ-pores around its middle region. These spores are distributed by air currents and are capable of germinating on other wheat plants. The resulting hyphae penetrate the leaf through a stoma, spread through the mesophyll, and produce new uredospores in a very short time under favourable conditions. Thus the uredospores serve for the rapid propagation of the Fungus, during early summer.

44. Teleutospores

Later in the summer, the sori which have been producing uredospores now give rise to another kind of spore—the **teleutospore** (Fig. 400, D). Each teleutospore terminates a hypha and consists of two cells. Each cell has two nuclei at first, but these later fuse, and so the mature spore has two uninucleate cells protected by a common thick, black wall. This black colour serves to distinguish the teleutosorus from the uredosorus, and gives the name black rust of wheat to the disease caused by *Puccinia graminis.* The teleutospores are essentially resting spores, and will only germinate after they have undergone a period of rest, usually through the winter, either in the soil or on the straw.

45. Basidiospores

When they germinate in the spring, each of the two cells puts out a hypha into which the fusion nucleus passes and divides twice so that four nuclei are formed. Each hypha septates to form a row of four uninucleate cells. This row of cells is a **basidium.** From each cell of the basidium a small outgrowth, a **sterigma,** arises. The tip of each sterigma swells and the nucleus of the cell passes into the swelling which is then abstricted as a **basidiospore** (Fig. 400, E). The basidiospores are dispersed, and may alight on barberry plants. On germinating, the hypha produced is capable of piercing the cuticle of the barberry leaf, and, spreading in the mesophyll, it ultimately produces a mycelium which develops spermogonia. Thus the life-cycle is completed.

46. Control of the Disease

The regular alternation of the Fungus between the two hosts, barberry and wheat, is essential if the rust is to persist. Clearly, therefore, one method of controlling the Fungus is to eradicate the barberry bushes. Long before the true nature of wheat rust was known, its prevalence in the neighbourhood of barberries was observed, and steps were taken to extirpate these bushes in order to control the rust. The measures met with much success and yet in some areas where barberries are absent, the rust appears on the wheat year after year with almost unfailing regularity. It is possible that this is due either to uredospores which may retain their vitality from one season to another where winters are mild, or to aecidiospores which may be wind-borne over long distances and so infect wheat in areas remote from barberries.

47. Physiologic Races

Puccinia graminis exists in a great number of physiologic forms or races which cannot be distinguished on morphological grounds, but which possess distinct infection capacities. All the races infect the barberry, but whereas one group of them can parasitise rye, barley, and some grasses but not wheat, another group attacks wheat, and a still further group oats. Thus uredospores produced by the mycelium in a wheat plant will infect wheat, they will not infect oats, whilst those produced on rye will not infect wheat. The occurrence of physiologic races of this type is not uncommon amongst the parasitic Fungi. We see here in *P. graminis* a very complex life history, a necessity for two host plants and the existence of physiologic races, all expressions of an extreme specialisation. *P. graminis* is an obligate parasite. The extreme obligatory nature of the parasitism is exemplified by the behaviour of the Fungus in some varieties of wheat that are immune to rust, and is the cause of this immunity. In these immune varieties, infection and penetration of the wheat leaf occurs in the usual way, but the Fungus kills the surrounding host cells, and further growth of the Fungus is thereby prevented, the hyphae being unable to absorb food from the dead cells of the host.

The extreme specialisation of *P. graminis* forms an interesting contrast with another rust fungus, *P. malvacearum*, the cause of hollyhock rust. Here all the parasitic stages of the life history can occur on one plant, whilst the Fungus is not confined to a single species. *Althaea, Malva, Abutilon, Lavatera* (all members of the Malvaceae) can be attacked. On these plants an intercellular mycelium in the leaf and stem produces small groups of hyphae beneath the epidermis of the host and a cushion of two-celled teleutospores is formed which bursts the epidermis. The teleutospores germinate in the teleutosorus, each cell of the teleutospore producing a basidium that bears four basidiospores. The basidiospores so formed can infect any of the possible host plants of the

Fungus. The life history is relatively simple. There are no spermatia, no aecidia, and no uredospores. There is no extreme physiological specialisation such as that in *P. graminis* which has resulted in the existence of several biological strains or races.

PSALLIOTA CAMPESTRIS—THE MUSHROOM

48. General

Psalliota is a genus included in a large family that comprises most of those Fungi popularly known as toadstools and mushrooms; themselves part of a still larger group, the **Basidiomycetes.** Many of the toadstools and mushrooms are saprophytes, and are to be found in abundance in damp woods where the soil is rich in organic material, but some are parasitic, and injurious to trees which they attack. Apart from this, they all closely resemble each other in structure, and in the general course of their life history. *Psalliota campestris* is the edible mushroom.

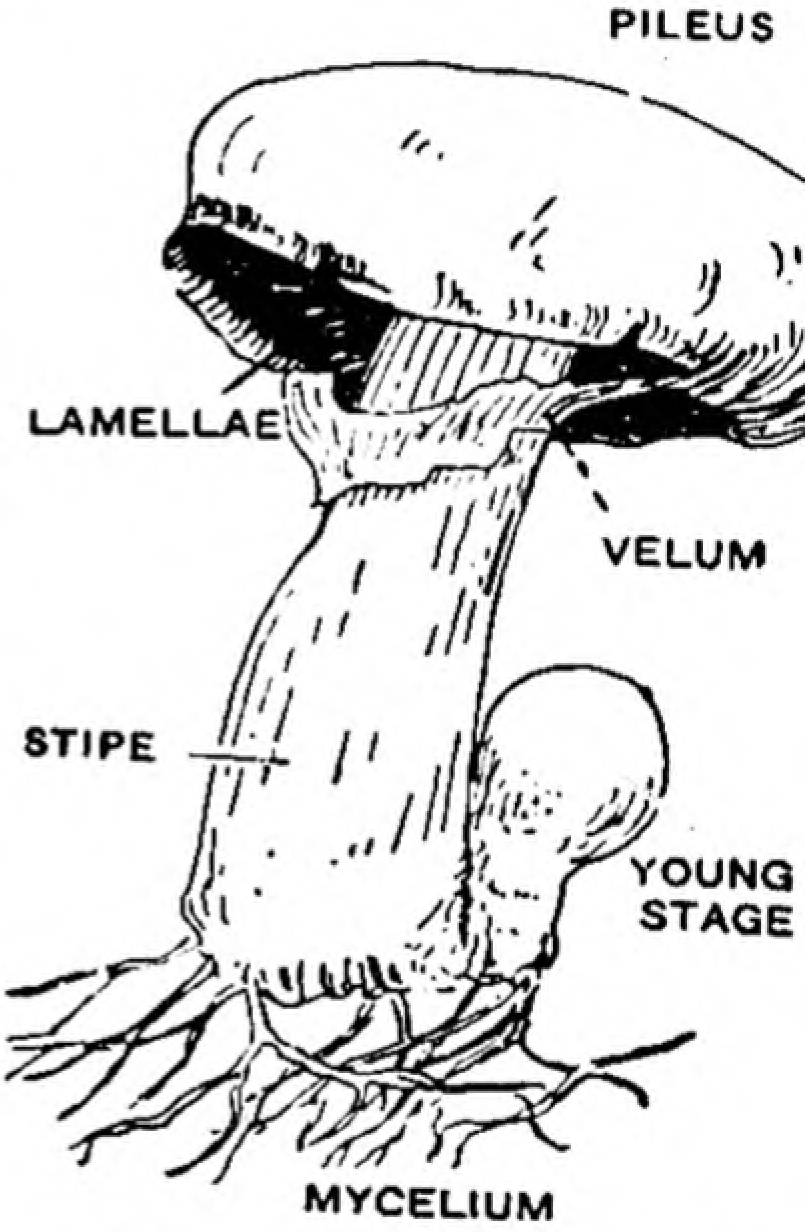

Fig. 401. THE MUSHROOM.

49. Habit and Structure

The mushroom is a saprophyte.* It lives on decomposing organic substances (humus), chiefly in meadows and pastures. The part of the Fungus which is seen above ground—the part which is called the mushroom—is really concerned with the reproduction of the Fungus (Fig. 401). The vegetative portion consists of hyphae which ramify through the substratum and absorb the soluble organic compounds from it, on which the Fungus lives. These hyphae are septate, and the cells are multinucleate. Together they form a loosely-matted mycelium, in which, however, hyphae may run in strands, with anastomoses between them.

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* It has been suggested that *P. campestris* is not truly saprophytic, but that the mycelium forms an association with the roots of the grasses among which it grows.

50. Reproduction

Mushrooms can be propagated vegetatively by means of portions of the mycelium, transferred to other suitable substrata. The "bricks" of commerce are dried compact masses of mycelium and organic substratum.

In nature, however, reproduction is effected by means of basidiospores produced in astronomical numbers by the reproductive bodies or "fructifications" which appear above ground.

The **fructification** makes its appearance on a strand of the mycelium as a rounded or pear-shaped, whitish body, consisting of a web of hyphae (Fig. 402). As growth proceeds, an upper region becomes distinguishable, and the fructification is now shaped something like a miniature "cottage-loaf." The upper portion grows at a greater rate than the lower, and develops into the familiar umbrella-shaped **pileus,** whilst the lower portion is the **stipe.** Embedded in the young pileus, before it expands into the umbrella-shaped structure, we find an annular cavity. In the roof of this cavity the **lamellae** or **gills** are differentiated, and its floor becomes stretched as the pileus expands, and is finally ruptured, forming the ring or **velum** on the stipe. The mature fructification is now a massive organ. The upper surface of the pileus is more or less rounded and convex. Its under surface bears a large number of delicate vertical plates radiating from the stipe to the edge of the pileus. These are the gills or lamellae. They are flesh-coloured when young, but become a chocolate-brown when fully developed. Encircling the stipe, close to the attachment of the pileus, is the ring.

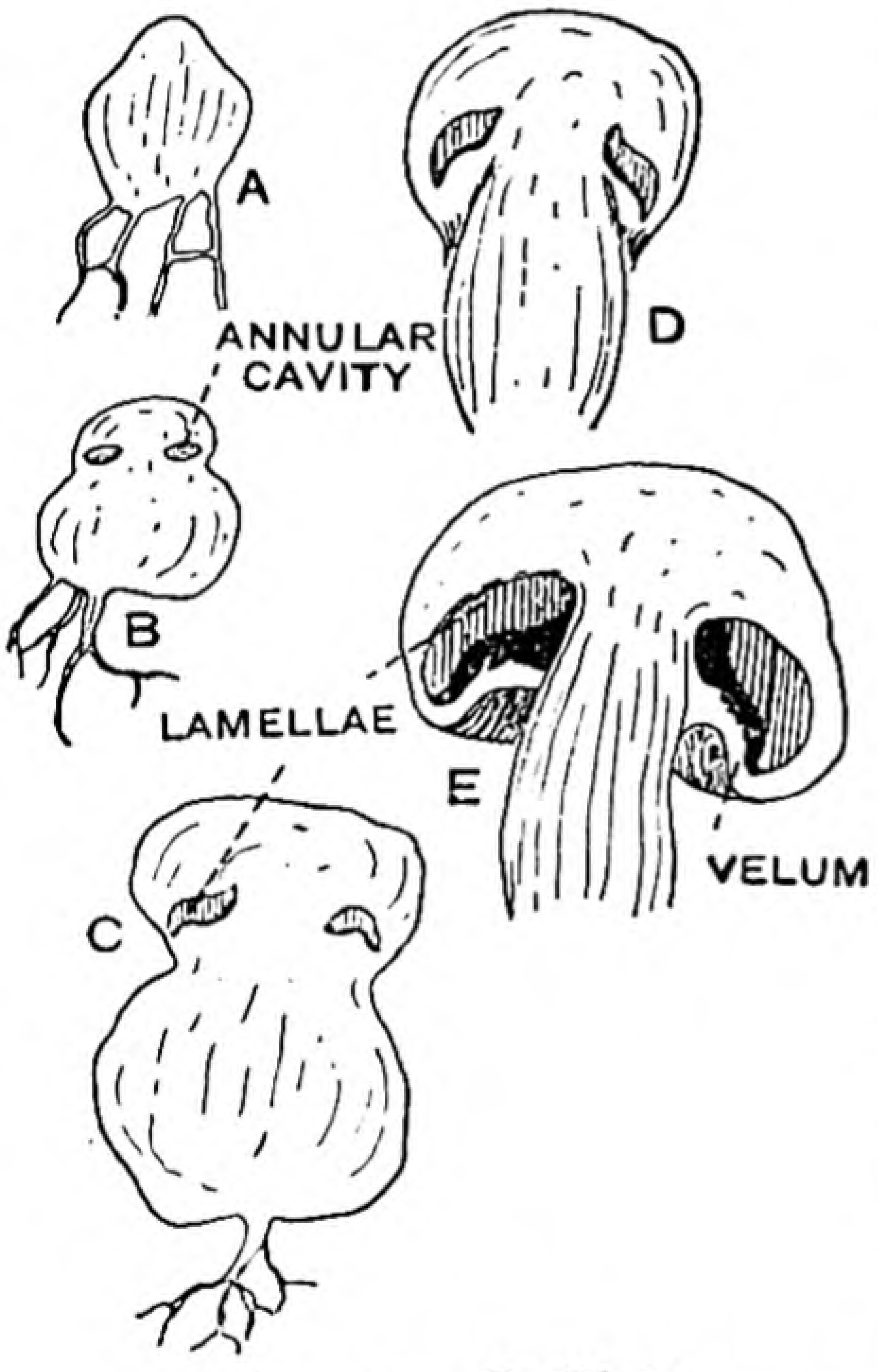

Fig. 402. *Psalliota.*
Stages in development of fructification. (Diagrammatic longitudinal sections.)

51. Structure

Microscopical examination shows the fructification to be composed of interwoven hyphae resembling those of the vegetative mycelium. The central region of the stipe consists of more loosely interwoven hyphae with air-spaces between them, and usually distinguished as the medulla from the outer cortical region of more densely compacted hyphae. It must be realised, however, that the " medulla " and " cortex " here are false tissues, built up of fungal hyphae, and are not to be compared with the tissues so named in the higher plants.

These two regions can be traced up into the pileus, but in the formation of the gills, the hyphae are more closely compacted. A tangential section of the pileus cuts the gills at right-angles to their flat surfaces. If such a vertical section of a gill is examined under the microscope (Fig. 403) it is possible to distinguish (*a*) a central core of interwoven hyphae known as the **trama**; these hyphae curve outwards towards each surface of the lamella and end in small cells which form what appears to be a tissue (*b*) the **subhymenial layer**; finally the hyphae terminate in slightly elongated cells, somewhat club-shaped, forming the superficial layer of the gill, called (*c*) the **hymenium.** These cells are the **basidia.** It is doubtful whether any of them are barren in *Psalliota*, they are at least all potential basidia, but in other toadstools there may be barren paraphyses amongst the basidia.

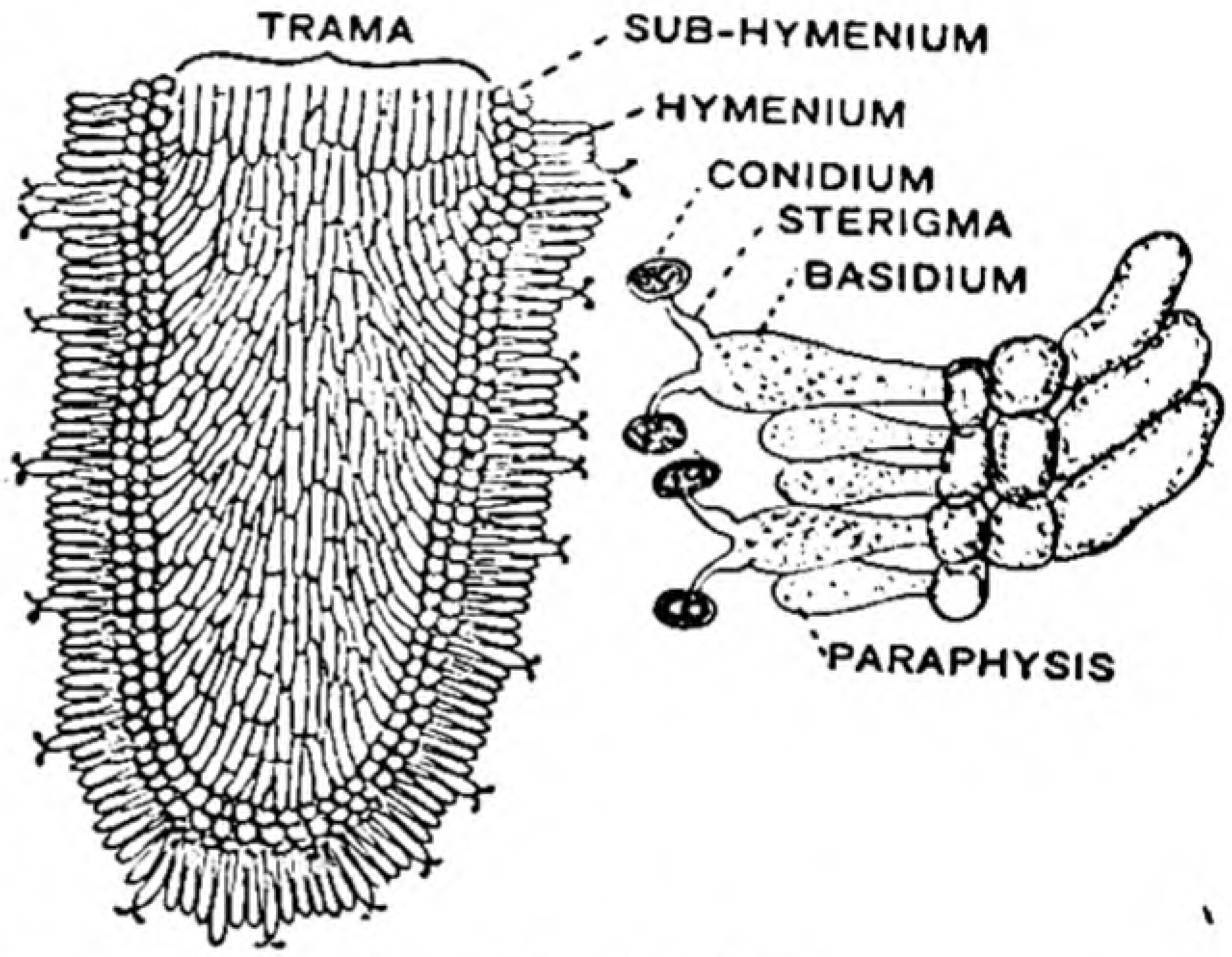

Fig. 403. *Psalliota.*

Section across one of the gills. The diagram to the right represents the hymenium and sub-hymenium more highly magnified.

The edible mushroom exists in at least two varieties. In the common wild variety each basidium puts out from its apex four slender processes called **sterigmata.** From each sterigma a small rounded spore is abstricted. In the cultivated mushroom, of which there are several forms in common use, only two sterigmata are put out, and therefore only two spores abstricted.

52. Basidiospores, Germination

The basidiospores are produced in great abundance. This can be demonstrated by laying a ripe pileus for some time on a sheet of paper. A print of the under surface of the pileus is obtained owing to the thick deposit of the spores. The spores when ripe fall off, and, if they reach a suitable soil, they germinate.

The earliest stages of spore germination have not been observed, and under carefully controlled conditions single spores usually fail to germinate. When large numbers of spores are " sown " together a mycelium is produced.

53. Basidiomycetes, Cytology

The cells of the mycelium of *Psalliota* contain up to twelve nuclei. The cells of the fructification contain rather fewer nuclei, and the number becomes less as one approaches the sub-hymenium. Here there are only two nuclei in each cell, and two in the young basidium. In the latter these two nuclei fuse to give a single diploid nucleus. This later undergoes meiosis and so four haploid nuclei are produced. These nuclei pass through the sterigmata and each becomes the nucleus of a basidiospore, which therefore contains a single haploid nucleus.

In the Ascomycetes we saw a gradual loss of sexuality, resulting eventually in the formation of an ascus and ascospores without the intervention of any sexual process. Always, however, ascus formation appears to involve the association and ultimate fusion of at least two nuclei. Again in the Basidiomycetes we get at some stage before basidium-formation an association of nuclei followed later by nuclear fusion in the early stages of development of the basidium. This involves the formation of a diploid nucleus by the fusion of two haploid nuclei, and is followed by meiosis, so that uninucleate haploid basidiospores are produced. We cannot distinguish male and female gametes and nuclei and therefore cannot call this process one of true sexual reproduction, although in *Puccinia* with its + and — strains there is a condition of affairs not altogether dissimilar to that in *Mucor*.

BACTERIA

54. General

The Bacteria are sometimes referred to as the Schizomycetes or Fission-Fungi because they usually multiply by fission, and occasionally they are linked with the Cyanophyceae (Blue Green Algae), which have a similar method of multiplication, to form the Schizophyta. They constitute a group of extremely minute organisms without chlorophyll, and leading a parasitic or saprophytic life. They are of especial interest because of their physiological rather than their morphological features. The Bacteria are commonly unicellular, but the cells may be aggregated into small filaments, plates or irregularly shaped groups. They occur in almost all situations and are not readily killed by extremes of temperature. Some can survive exposure to the temperature of liquid air and others can thrive at temperatures as high as 70° C., whilst the spores of many can withstand boiling water.

55. Structure

The Bacteria are extremely minute, the cell often being less than 0·001 mm. in diameter, and our lack of detailed knowledge of their structure is in part a result of their extremely small size.

Each cell has a superficial limiting membrane surrounding a protoplasmic mass, in which chromatin granules commonly occur. No organised nucleus has been observed and the chromatin granules probably represent a nucleus. No plastids and no chlorophyll are present, but a variety of pigments do occur, so that the Bacteria are variously coloured. Many of the Bacteria have cilia and are motile. The Bacteria are subdivided according to the shape of the cell (Fig. 404). The cells may be spherical (Cocci), rod-shaped (Bacilli), spiral (Spirilla). Occasionally large numbers of bacterial cells are held together in mucilage and this is spoken of as the zoogloea condition (Fig. 405).

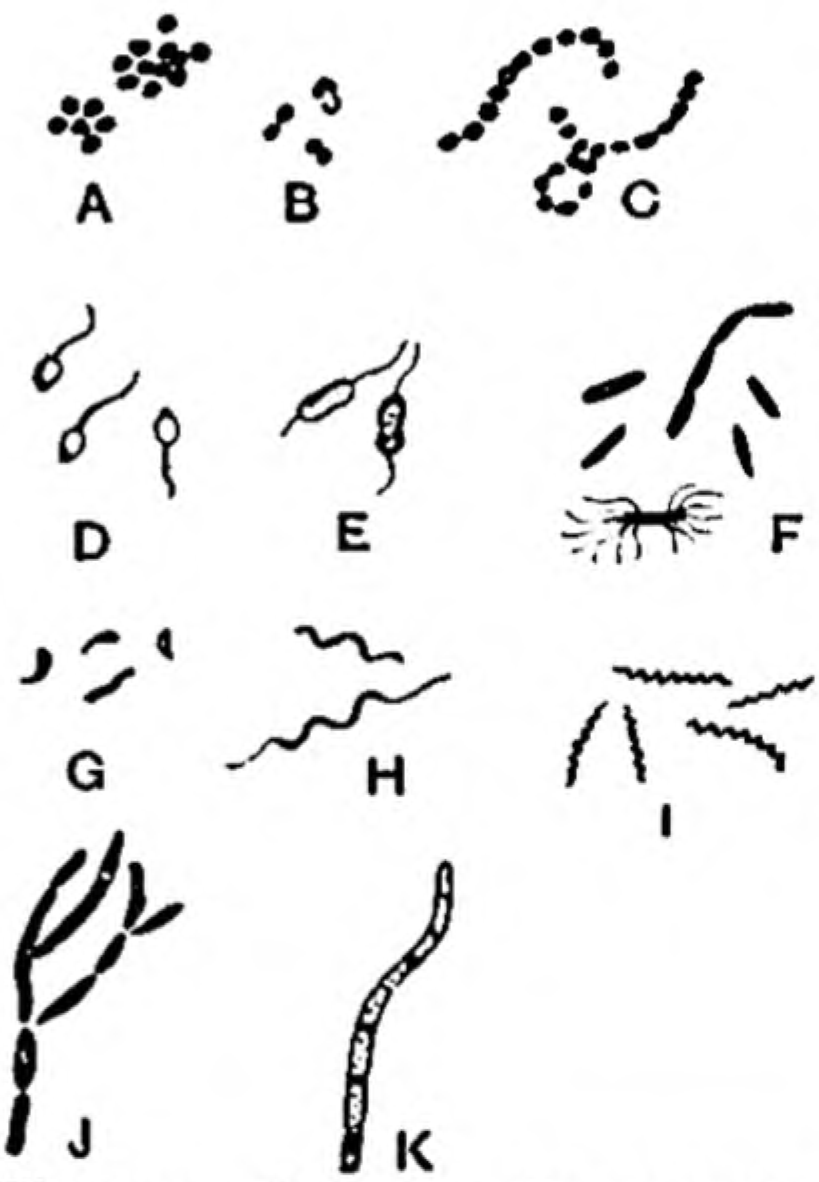

Fig. 404. FORMS OF BACTERIUM-CELLS. (× 1,500.)

A, Staphylococcus from a boil: B, Diplococcus: C, Streptococcus, of blood-poisoning; D, Nitrosomonas; E, Biflagellate Bacteria; F, Bacilli, the flagellated one is B. typhosus of Typhoid Fever: G, Commas: H, Spirillum; I, Spirochaete pallida of Syphilis: J, Cladothrix dichotoma; K, Beggiatoa alba (the granules are deposited sulphur).

56. Reproduction

There are two methods of reproduction. Both are asexual. In the process known as "fission," the parent-cell undergoes division into two daughter-cells. A coccus cell becomes constricted and divides into two; a bacillus divides transversely. When active, many Bacteria can divide in this way once every half-hour, so that in twelve hours one single organism will have produced over sixteen million descendants. When suitable food-material is available multiplication of this type proceeds actively, but usually not indefinitely. Various external checks control the increase. With many Bacteria light inhibits growth, whilst commonly their growth is checked by some of their own metabolic products. Usually, of course, lack of food-material sooner or later will limit the growth of the bacterial colony.

The other method of reproduction, which is a method of resting rather than of multiplying, is that of " **spore**"**-formation** (Fig. 405). It is commonly seen in bacilli, and as a rule it takes place in the zoogloea stage. The protoplasmic contents of the cells, starting from a small centre, gradually round themselves off, and aggregate in the middle of the cells. A new cell-wall is then formed round the protoplasmic mass. When fully formed, this cell-wall is extremely firm and resistant. Thus the " spores " are produced inside the cells (endospores), usually one in each cell, but sometimes more than one. The spores can withstand great extremes of heat and cold without injury, some of them being able to withstand boiling, or immersion in liquid air for a considerable period. They occur almost everywhere, in the air, in dust, etc., and this explains why, when suitable substances are exposed to the air, bacterial colonies soon appear on them. They may remain quiescent for a considerable time if the conditions are unfavourable, but are eventually set free by the decay of the walls of the parent cells. When a spore germinates, the outer membrane is ruptured, and the contents escape as an ordinary bacterium-cell.

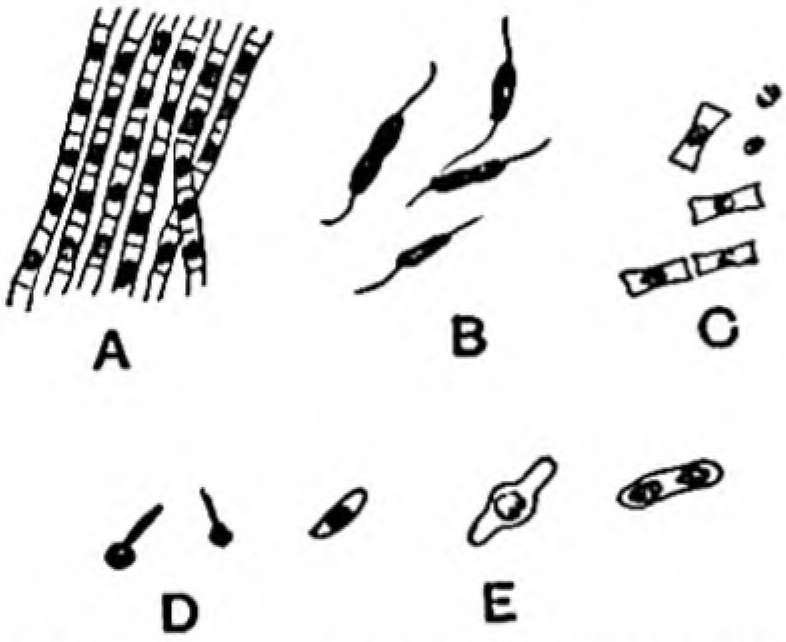

Fig. 405. SPORE-FORMATION IN *Bacteria*.

A, Zoogloea stage, with spore-formation ; B, Motile stage of A ; C, Bacillus anthracis, of Anthrax ; D, Bacillus tetani, of Lockjaw ; E, Bacillus mycoides.

57. Bacillus subtilis

Bacillus subtilis, the hay bacillus, will serve as an example. If hay is chopped up and boiled in water and the decoction kept for some little time, numerous bacillus cells can be recognised if the fluid is examined under a high power of a microscope. Each cell is a tiny rod-shaped body having the structure described in § 55. It bears a number of cilia. In this stage the cells multiply by fission, but after a time they pass to the surface and form a scum (zoogloea stage). If this is examined the cells will be found aggregated into long filaments embedded in a mucilaginous substance, formed by the disorganisation of the outer layers of the cell-membranes. It is in this stage that the spores are developed. They are extremely resistant, and can withstand boiling for a considerable time. They germinate in the usual way in a suitable medium. It is interesting to note that a single boiling is not sufficient to destroy the bacterial spores. This has an important bearing on the methods adopted for sterilising substances, *i.e.* freeing them from Bacteria, Fungi, and other micro-organisms.

58. General Physiology of the Bacteria

A manifold diversity of metabolic processes is exhibited by various Bacteria. They have no chlorophyll, and so cannot carry out the photosynthesis of carbohydrates. A few, however, are able to build up carbohydrates from carbon dioxide in the absence of both light and chlorophyll. The majority obtain their energy by the partial or complete oxidation of carbohydrates (obtained either from living or dead organic matter), but a few oxidise other compounds, e.g. ammonium, hydrogen, etc., and utilise the energy liberated in these oxidations. They mostly require a supply of elaborated nitrogenous compounds, but some can utilise gaseous nitrogen. Some can live only in the presence of oxygen, and others only in its absence. All of them can absorb food-material only when it is presented to them in solution.

59. Special Physiology of Bacteria

A few of the Bacteria are autotrophic, *i.e.* they build up their substance by the assimilation of simple inorganic materials. The majority, however, have not the ability to assimilate purely inorganic substances. They require a supply of organic substances and are said to be heterotrophic.

The heterotrophic Bacteria can be conveniently subdivided according to their mode of nutrition:—

(1) PARASITIC BACTERIA. These forms parasitise other living organisms and many of them cause disease in plants, animals, and man. Disease causing Bacteria are frequently termed pathogenic. Not all parasitic Bacteria are pathogenic. Many inhabit the mucous-membranes of the mouth and nose of man without doing any harm. Others, however, enter the tissues and are the cause of disease—thus anthrax is caused by *Bacillus anthracis* and lockjaw by *Bacillus tetani*. The serious consequences of infection by these Bacteria are usually due to poisons or toxins that they liberate in the tissues of the host. Frequently the presence of such a toxin stimulates the host to produce an anti-toxin that has the power of neutralising the toxin. Many sera used either to cure or to prevent bacterial diseases are preparations of anti-toxin.

A number of the pathogenic bacteria are obligatory anaerobes, *i.e.* they can exist only in the absence of oxygen. *B. tetani* is of this type, but most of the animal pathogens are facultative anaerobes.

Bacterial diseases of plants are not so numerous as those of animals. They do occur, however, and wilt disease of cucumbers, black rot of Cruciferae and soft rot of turnips and many other vegetables represent a few of the commonest bacterial diseases of crop plants. These parasites are, of course, entirely dependent on their hosts for a supply of food.

(2) SAPROPHYTIC BACTERIA. These only live on dead organic matter and together with other heterotrophic organisms (small animals and Fungi) are important agents in promoting the processes of decay. They absorb complex organic substances, and partially oxidise them, or sometimes break them down in the absence of oxygen. The decomposition of animal and plant remains, that takes place apparently spontaneously, is in fact due to Bacteria and similar organisms. Certain of the oxidations and fermentations promoted by the Bacteria are utilised by man. Hot beds of manure are used by the gardener. The heat generated in the manure heap represents a liberation of energy by the micro-organisms (including Bacteria) inhabiting the manure. The acetification of alcohol with the production of acetic acid is brought about by *Acetobacter aceti* and other Bacteria, and is the basis of vinegar manufacture.

Of special interest are a few saprophytic Bacteria with the ability of fixing free nitrogen and reducing it, with the formation of organic nitrogenous compounds. Two common Bacteria found living free in the soil and capable of " fixing " nitrogen are *Azotobacter chroöcoccum* and *Clostridium Pasteurianum*. They obtain their energy from carbohydrates in the soil; *Azotobacter* oxidises them and is aerobic, while *Clostridium* ferments them and is anaerobic, only flourishing in the absence of oxygen or in the presence of an abundance of *Azotobacter*, which removes all the free oxygen. The energy so obtained is used by both organisms to " fix " atmospheric nitrogen and convert it into organic nitrogenous compounds. The nitrogen compounds formed on nitrogen fixation are finally set free in the soil either by the death of the Bacteria, or by secretion by the living ones. Whereas *Azotobacter* and *Clostridium* are free-living, saprophytic Bacteria, *Bacillus radicicola*, another Bacterium capable of fixing nitrogen, inhabits the roots of leguminous plants (p. 199).

It was for a long time recognised that leguminous plants would readily grow in a medium containing little or no *combined* nitrogen, and that the soil was often richer in nitrogen after a leguminous crop had been grown. These facts, which were at first extremely puzzling, have now been explained. Numerous small nodules or tubercles are found on the roots of these plants (Fig. 152). When the nodules are examined they are seen to be filled with small unicellular bodies called **bacteroids.** These are a form of *Bacillus radicicola.*

Cells of this Bacterium are usually present in the soil. They infect the roots of any leguminous plant through the root-hairs, and pass to the adjoining cells. These cells are stimulated to divide repeatedly, so that swellings or nodules are produced on the roots. Microscopic examinations of sections of nodules (Fig. 152, B) show a central mass of host-cells occupied by the Bacteria which assume various shapes and form bacteroids. The nuclei of the host-cells stain deeply for chromatin, suggesting that they are well nourished. It is interesting to contrast this condition with that of the nuclei of cells attacked by parasites. The Bacteria in the root cells are able to fix gaseous nitrogen, which diffuses to them through the intercellular spaces of the plant. Some of the nitrogen fixed in this way is used by the Bacteria, but a proportion of it is made available to the green plant. Just how the transfer of nitrogenous substances from the bacterial cells to the host are made we do not know. Possibly the Bacteria secrete nitrogen compounds into the cells of the nodule, or the Bacteria may die and their products be added to the contents of the host-cell. Again, the cells of the nodule may digest the bacteroids. It is certain, however, that the Bacteria render the leguminous plant independent of an external supply of nitrates. The legume can obtain its nitrogen from the air through the agency of *Bacillus radicicola.* The Bacteria obtain their supply of carbohydrates from the host in which they live. Clearly then, the Bacteria benefit from association with the green plant. It is equally clear that the legume benefits from its association with the Bacteria. Here, then, we have an intimate association of two organisms which is mutually beneficial. Such an association is called symbiosis.

Several biologic races of *B. radicicola* exist, so that a strain isolated from clover will not infect lucerne, that from lucerne may not infect peas, and so on. Different races, too, differ in the efficiency with which they fix nitrogen.

The autotrophic Bacteria include the nitrifying Bacteria which are found in the soil. Of these, *Nitrosomonas* and *Nitrobacter* oxidise ammonia and nitrite respectively. These oxidations can be represented by the equations—

$$2\,NH_3 + 3\,O_2 \rightarrow 2\,HNO_2 + 2\,H_2O + 179 \text{ Calories}$$
$$2\,HNO_2 + O_2 \rightarrow 2\,HNO_3 + 18 \text{ Calories.}$$

The ammonia utilised in this way is derived from the breakdown of plant and animal remains, and results in nitrate being formed in the soil. Such a conversion of complex nitrogen compounds to nitrate, accomplished in stages by different soil organisms, is spoken of as nitrification. The resulting nitrate can be absorbed by the roots of green plants.

We may regard the oxidations brought about by *Nitrosomonas* and *Nitrobacter*, with the consequent liberation of energy, as constituting an abnormal type of respiration. The energy thus liberated is used by these Bacteria in building up organic compounds from carbon dioxide. The process is spoken of as chemosynthesis in contrast to the photosynthesis of green plants. In this respect these Bacteria are unique among non-chlorophyll containing plants as they do not need to be supplied with carbohydrates. Although they are tolerant of these substances in nature, they can only be grown artificially in media devoid of organic matter.

Usually present in the soil, too, are certain denitrifying Bacteria, capable of reducing nitrates to gaseous nitrogen. This process occurs actively only in the absence of oxygen.

60. The Nitrogen Cycle

It is largely due to the activity of the nitrogen-fixing Bacteria and the nitrifying Bacteria that we get in nature a continual circulation of nitrogen. This can be represented conveniently by the following scheme:—

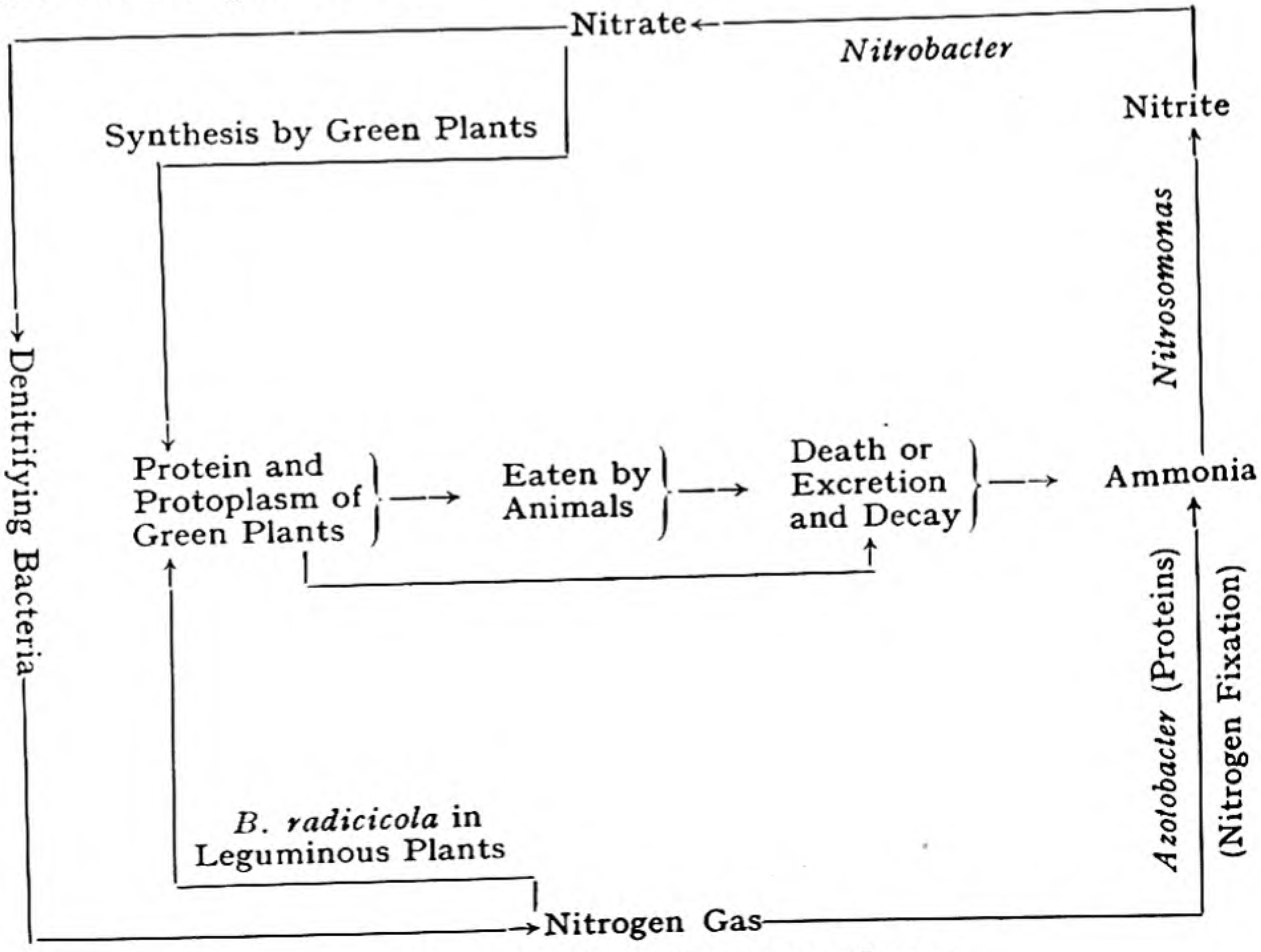
Nitrate
Nitrobacter
Nitrite
Synthesis by Green Plants
Nitrosomonas
Denitrifying Bacteria
Protein and Protoplasm of Green Plants
Eaten by Animals
Death or Excretion and Decay
Ammonia
Azotobacter (Proteins)
(Nitrogen Fixation)
B. radicicola in Leguminous Plants
Nitrogen Gas

Fig. 406. THE NITROGEN CYCLE.

61. The Carbon Cycle

Autotrophic and heterotrophic organisms by their combined metabolic processes are also concerned in the circulation of carbon. We have seen that green plants synthesise complex organic substances from carbon dioxide and water in the presence of light. Certain Bacteria also are capable of utilising other sources of energy for the same purpose. A considerable proportion of these organic compounds, which form the tissues and food reserves of plants, and of the animals which feed on them, consist of carbon. By progressive degradation these organic compounds are finally oxidised to carbon dioxide. Hence there is no accumulation on the earth's surface of the tissues of dead animals and plants. Their constituents are rendered available to successive generations of green plants, and hence to animals, and so the cycle continues.

62. The Sulphur and Iron Bacteria

The nitrifying Bacteria are not the only types that are autotrophic. The sulphur Bacteria oxidise sulphur compounds and the iron Bacteria oxidise ferrous to ferric iron. The activity of the iron Bacteria often results in the production in water of flocculent masses of iron hydroxides which may block water pipes. Both of these types of Bacteria promote oxidations and utilise the energy set free in these oxidations to reduce carbon dioxide to organic compounds, *i.e.* they carry on a process of chemosynthesis of organic substances. Less common Bacteria appear able to oxidise methane, carbon, and even hydrogen.

63. Culture of Fungi and Bacteria

Many Fungi and Bacteria can be cultivated in artificial media, and their growth under carefully controlled conditions studied. For this purpose a pure culture of the Fungus or Bacterium is necessary. The Fungi are generally cultivated on a jelly medium with a basis of either gelatine or agar-agar, to which various nutrients have been added. A hot solution of gelatine or agar-agar containing nutrient substances is poured into special dishes (Petri-dishes), with loose-fitting lids, or into flasks or test-tubes that are then plugged with cotton-wool. The vessels containing the medium are then treated in such a way that the contents are sterilised, *i.e.* freed from all living organisms. The sterilisation is generally effected by heating the vessel containing the medium to a temperature higher than that of boiling water (usually by means of an autoclave). Simple boiling is, as we saw earlier, not sufficient, as many bacterial spores can survive exposure to a temperature of 100° C. Instruments that are to be used may be sterilised either by heating in superheated steam, passing them through a flame, or by washing them with special disinfectants (germicides). When it is necessary to do so, air may be sterilised by drawing it through a plug of cotton-wool which filters out all fungal spores or bacterial cells and spores initially present in it.

When a dish of medium has been sterilised it is allowed to cool, when it sets to a jelly, and it is then infected with the Fungus. The infection is carried out by transferring to the medium a few spores, or a piece of fungal mycelium on a previously sterilised needle, precautions being taken to prevent the access to the medium of foreign spores that may be present in the air. Less frequently Fungi are grown in liquid media. Bacteria may be grown in solid or liquid nutritive media, but owing to their small size, their isolation in pure culture is a matter of difficulty. A drop of material containing Bacteria is mixed with a sterilised jelly medium which has been made fluid by warming. This separates the individual Bacteria. The fluid medium is then carefully poured into a Petri-dish and incubated at the correct temperature. The liquid cools and sets again to a jelly, and each individual Bacterium gives rise to a separate colony of cells. A fresh culture can be prepared by using one of these colonies as the source of infection. In this way pure cultures are obtained, and this is often a necessary prelude to the identification of pathogenic Bacteria. Owing to their small size, microscopic examination often fails to establish their identity, and their identification depends on the chemical reactions that they promote when growing on different types of media.

64. Viruses

We have seen that many diseases of plants and animals are caused by the attack of parasitic Fungi and Bacteria. A large number of plant and animal diseases are caused not by Fungi or Bacteria, but by what are known as viruses. Viruses are particulate, and the size of the particles is determined by observing their ability to pass through filters whose pore-size is known. Many virus particles are less than $\frac{1}{100000}$ mm. in diameter. We do not know if the viruses are all living or non-living; but substances crystalline in nature, and with all the properties of a virus have been prepared, and so it appears likely that the viruses are not living organisms. They have, however, the ability to "grow," or at least to increase in amount, when in the tissues of a suitable host. Possibly the virus stimulates the host cells to produce more of the virus.

Many important plant diseases are due to virus. Of these we may mention sugar-cane, cucumber, and tobacco mosaic, tobacco and cotton leaf curl, and spike disease of *Santalum*. The frequent occurrence of virus-induced mosaic disease, in which the foliage has a characteristic mottled appearance, is worthy of note, as certain types of variegation (e.g. in *Abutilon* and *Aucuba japonica*) are due to viruses, but in these cases the virus does not seem to affect the general health of the plant adversely. Often, however, the vigour of the plant and its yield are greatly reduced. The virus appears to invade all the vegetative parts of the plant so that when the plant is normally propagated vegetatively (e.g. potato) there may be an accumulation of virus from year to year within the plant, leading to a gradual loss of vigour and degeneration of the stocks of that plant. This has happened with many varieties of the potato. Virus diseases are transmitted by sap-sucking insects, chiefly *aphids*. When sap from an infected plant is injected into a healthy one, the latter soon develops symptoms of the virus disease.

65. Plant Diseases and Disease Control

Any morbid condition of a plant or part of a plant with special symptoms and to which a name (usually descriptive) has been given is popularly known as a disease. We have seen that many plant diseases are caused by the attack of parasitic Fungi and Bacteria and by viruses. Many diseases are not of this type, but are of the nature of physiological disorders. We have already seen how in water culture experiments a deficiency of iron may give rise to a condition known as chlorosis. Deficiency diseases of this nature are common in crop plants. Leaf scorch of fruit trees, in which the apices and margins of the leaves wither, is due to a deficiency of potash, and sulphur deficiency is the cause of "tea yellows." Many deficiency diseases can be prevented by correcting by suitable manuring the nutritional deficiency which is the cause of the disease. Other physiological disorders, e.g. a spotting of the flesh of apple fruit known as bitterpit, and "spraing" of potato tubers, cannot be ascribed to any particular nutritional deficiency, and their precise cause remains unknown.

Fungus diseases are frequently controlled by spraying the host plants with a fungicide, a preparation which is toxic to the Fungus, but at the concentration used, harmless to the host plant. Commonly employed fungicides are lime-sulphur and Bordeaux mixture, and in their application the aim is to leave a thin deposit of fungicide over the surface of the plant so that spores alighting on the leaves, etc., may germinate, but the hyphae are killed by the toxic fungicide. The most promising method of combating diseases is the use of immune or resistant varieties of crop plants.

PART V

CHAPTER XXI

THE ECOLOGY OF PLANTS

1. Plant Ecology

Plant Ecology is the study of plants in relation to their environment. The study may be divided into two fairly well defined sections, Autecology and Synecology.

(*a*) AUTECOLOGY. This is concerned with individual plants throughout their life history in relation to the habitats in which they grow. It presents a series of problems involving a knowledge of nutrition, growth, reproduction, development, etc.

Some species of plants are confined to one type of habitat. Other species occur on a range of habitats, but may consist of forms which differ somewhat from each other, according to the type of habitat in which they are found. These varying forms of a species are called ecotypes. They are the result of the reaction of a species to its environment. The differences often tend to disappear if the ecotypes or their progeny are brought together and grown on a common habitat. Some species never form ecotypes.

(*b*) SYNECOLOGY. Synecology is the study of plant communities. Plants in nature tend to grow in association with other plants, and not as isolated individuals. The plants in a given community may have similar life-forms, that is, have superficial resemblances or structural characters in common. On the other hand, more than one type of life-form may comprise a community.

In any community the relationship of the species to one another is approximately constant. In describing such a plant community it is essential to give the relative frequency of the species and their relation to each other.

Ecological maps represent the relationships of the different communities to each other.

2. Environment

The assemblage of factors that make up the environment of any particular piece of vegetation may be divided into climatic, edaphic (e.g. soil), and biotic (*i.e.* the effect of other organisms, including man). The effects of single factors cannot always be considered separately. They are interdependent. Climate affects soil, soil type may determine the intensity of certain biotic factors, and so on.

(*a*) CLIMATE. In studying world vegetation it is clear that the distribution of the great plant communities of the world is correlated with climatic differences. The chief types of plant community are listed below:—

1. Tropical Forest.
2. Tropical Grassland.
3. Hot Desert.
4. Temperate Forest.
    - (*a*) Warm Temperate.
    - (*b*) Cool Temperate.
        - (i) Deciduous Summer Forest.
        - (ii) Coniferous Forest.
5. Temperate Grassland.
6. Tundra and Ice Desert.

The distribution of each corresponds to a fairly well defined climatic zone, the nature of which is determined chiefly by latitude, altitude and proximity or otherwise to large masses of water. One plant community gradates into another; the limits of each are not sharply defined, and so many intermediate vegetational types occur. Even within each type there is not complete uniformity. For example, in India, tropical evergreen forest is found in its highest development in the Malabar Region along the western coast, but in other regions, where long periods of drought occur, the forest may be mainly deciduous or give place to thorny scrub. In a particular region the natural vegetation may belong to a definite type, but it often happens that this has been replaced by an artificial type determined by man's activities (e.g. cultivated land). The more luxuriant the original vegetation, the more likely is this change to occur, although, by irrigation, many semi-arid regions, which would otherwise be left undisturbed, have been brought under cultivation. In a highly populated region relatively little of the primitive natural vegetation may survive, yet a large number of natural or semi-natural communities of plants, each with a characteristic appearance, may be distinguished, e.g. various types of forest, thorny scrub, grasslands of various types, vegetation of fresh water, salt-marsh, sand-dune and margins of rivers and lagoons. The existence of these is determined partly by local climatic factors and partly by edaphic (soil) conditions, whilst the effect of human interference is very often manifest.

Climatic Factors. India is a large country and shows very considerable variation in climate. About half of the total area is within the tropics, but in northern and north-western parts the climate ranges from sub-tropical to temperate. Of the climatic factors which affect plants the more important are temperature, precipitation (amount and seasonal distribution), light (intensity and duration) and wind. These in turn affect atmospheric humidity.

In the tropics and sub-tropics temperature and light are normally favourable to plant growth, and near the Equator there is little seasonal variation in either throughout the year. In such climates rainfall usually has the greatest influence in determining the type of vegetation. In India the rainfall is largely connected with the monsoons, particularly the south-west monsoon. The total annual precipitation varies from almost nothing in parts of the Indus plain to nearly 500 inches in a region of Assam. What is often of more importance to vegetation than the amount of precipitation is the duration of periods of drought. If a plant is unable, by some means or other, e.g. by losing its leaves, to survive the periods of drought to which it may be subjected, then inevitably it must disappear. It will usually be replaced by another species better adapted to such conditions.

Local climatic variations occur within a given region. The physical geography of the region may be such that small sheltered or exposed areas, or small areas of low or high rainfall, occur, and these variations may be reflected in the local vegetation. Altitude may have a very marked effect on climate and hence on vegetation. There is a steady fall in mean temperature with increase in the height of the land, so that even in tropical regions, such as Ceylon and South India, the hill-tops which rise to over 7000 ft. may have an almost temperate climate. It differs, however, from the temperate climates of northern and southern latitudes in being relatively uniform throughout the year.

(*b*) EDAPHIC FACTORS. Under edaphic factors we consider the effect of soil, subsoil and underlying rock on the vegetation. The soil is the portion of the solid substratum in immediate contact with the roots of the plants growing in it. The subsoil is below the root region, but the differentiation is not sharp and the roots of many plants may penetrate into what is generally termed subsoil.

(i) *The soil profile* is exposed and may be studied on the vertical sides of a pit dug through the soil. In it more or less definite layers may be recognised, beginning at the surface and progressing downwards. This stratification is the result of the action of various agencies such as weathering and the flora and fauna of the soil. Substances may be leached from the surface layers and deposited lower down in the form of a hard " pan " which may offer mechanical resistance to root growth. If such a pan exists it often marks the lower limit of the soil proper.

(ii) Just as *water* and *temperature* are of considerable importance in the way they affect the vegetation of a given area, so also these climatic factors operate in producing a definite soil type. Surface drainage water may bring about the transport of soils which are deposited elsewhere as alluvium and estuarine sand and mud. Rain may also act as a solvent for the soluble salts present in a soil, and carry the finer particles deeper below the surface, producing what is known as leaching of the surface layers. In the preceding paragraph mention has been made of pan formation by leaching. Soils which do not drain well may become waterlogged, and the formation of humus may be aided or hindered according to the amount of water present. Even the kind of humus produced varies according to water conditions. Chemical processes in soils may be inhibited at low temperatures and accelerated at high ones. At higher temperatures there will tend to be a greater rate of evaporation from the soil surface and from the plants, and the air above the soil will hold more water.

(iii) The *physical properties* of a soil have an important bearing on the amount of water it is able to hold. From this aspect soils may be classified into sandy soils, clay soils, etc. Loam is a mixture of sand and clay; marl of clay and limestone. Soils are subjected to mechanical analysis in order to discover the relative proportions of particles of different sizes. Water is held in the soil by capillarity and a certain amount of this water can be held against evaporation, depending on the structure of the soil, and the amount of colloidal, especially organic, material contained in it. Organic soils, in addition to capillary water, contain also water imbibed by the organic material.

In any soil no plant is able to use all the contained water. The amount of this non-available water varies with the soil and with the type of plant. It may be determined by the point at which a plant wilts, but with many plants such as xerophytes, this point is not readily discernible.

(iv) The *reaction* of a soil is usually expressed in terms of pH values. A " neutral " soil-water gives a pH7 (*i.e.* contains approximately 10^{-7} gm. per litre of free hydrogen ions), a decreasing index means increasing acidity, whilst pH8 indicates an alkaline soil-water in which hydroxyl ions are in excess of free hydrogen ions. " Indicators " for determining the pH value colorimetrically are sold. To some extent the vegetation reflects the pH of the soil, in that certain species can only tolerate acid soils, whilst others will only grow under alkaline conditions. Since calcium is the most abundant basic ion in our soils, plants which cannot tolerate the alkalinity which characterises basic soils have been termed calcifuge species.

(v) *The Chemical Nature of the Soil.* Except in a few instances, deficiency of soluble mineral salts is rarely a factor influencing plant distribution. A few substances such as common salt, carbonate of lime, humus, and pure quartz sand affect the vegetation-type produced.

Humus formation varies under different conditions. *Mild humus* (known technically as " mull ") is formed by the breaking down of plant remains and their incorporation into the soil by earthworms. Aerobic and nitrifying Bacteria are present. It is well aerated, and although showing a somewhat acid reaction, basic ions are present in good supply. Soil temperature and moisture are moderate. *Raw humus* (" mor ") possesses no earthworms and the vegetable remains show only slight decay. Nitrifying Bacteria are absent, and fungal hyphae predominate. Oxygen is deficient where the soil is waterlogged, and the soil reaction is extremely acid. Basic ions are in short supply in *acid peat*, which is developed under water or in very wet conditions where aeration is lacking, and over soils poor in mineral salts. *Fen peat* accumulates where the ground water is richer in soluble salts, especially calcium which neutralises the organic acids and may even render the peat alkaline in reaction.

(*c*) BIOTIC FACTORS. These include the influence of animals on vegetation. This influence may be exerted in various ways. Man, in various parts of the world has replaced the natural vegetation by one which ministers more suitably to his own needs, or he has adapted and modified the natural vegetation without destroying it. In many regions much of the original forest has been replaced by crops or grass. Grazing alone may be a potent factor in preventing the spread of forest at the expense of grassland and in promoting the extension of the latter. In some areas grazing, by its effects on unprotected competitors, may encourage the spread of shrubs which are armed with thorns. Animals also may play a part in the introduction of plants into new areas. For example, the rapid extension over large parts of India and Ceylon of the introduced shrub *Lantana aculeata* has been due to transport of its seeds by birds.

3. Vegetation

In tropical regions, wherever moisture is sufficiently abundant, forest was originally predominant. This had persisted with little change for very long periods and represented the climatic climax. In many areas the primary forest has been profoundly modified by man's activities. In some places, the original trees comprising the forest have been replaced by introduced species as, for example, by the planting of the rubber tree, *Hevea braziliensis*, in forest areas of Malaya, Ceylon and elsewhere. In others, cleared areas have been devoted to the cultivation of cereal crops. There are also tracts of country occupied by indigenous species, but subject to interference by man. Such tracts are said to bear a semi-natural vegetation.

Under natural conditions the vegetation occupying a given habitat at a given time may be regarded as that which is most suited to it. Generally it is in a state of equilibrium, and holds its own against invaders. Occasionally plants are introduced either naturally or artificially which are able to spread at the expense of the natural vegetation, and so upset the equilibrium. Sometimes a habitat may be suddenly denuded of its natural vegetation by natural (landslide, volcanic action, etc.) or by artificial means (railway cuttings, quarrying, etc.), or the change may be slow, as when streams cut back into peat and gradually drain it.

The species of plants which form the vegetation of a given habitat may be few or many, and the stability of the habitat is due to the effect of the balance between all the factors of the habitat (edaphic, climatic and biotic) and the individual organisms which compose it (competition, mutual accommodation, etc.). The plants which together form the vegetation of a habitat are collectively referred to as a *plant community*. Different plant communities may be distinguished not only by the fact that they are composed of different species, but also of different life-forms. Plants of widely separated species may correspond in certain morphological characters.

Vegetation types may be described according to their water-relations. Plants which live wholly or partially submerged in water are called *hydrophytes*, those which grow under permanently moist conditions, *hygrophytes*, plants which are subjected to alternating moist and dry conditions, *tropophytes*, and plants which can subsist with a small amount of water, *xerophytes*. Under the last-named are often included *halophytes*. Modifications of structure usually accompany these different types since transpiration is closely bound up with available water. Thus we have succulent xerophytes, including plants from such widely separated families as Cactaceae, Euphorbiaceae and Compositae. Drought-resistance is also seen in plants with reduced leaves, leathery leaves and woody shoots. Such modifications have been described as xeromorphic characters, but these do not always mean a xerophytic habit in the plant which possesses them.

Most plant communities are "*closed*" in that they cover the ground above it or occupy it with their roots below the surface. In "*open*" communities the individuals are spaced out, and hence the unoccupied spaces may be colonised by plants from outside. Open communities are therefore subject to change.

Observations on the colonisation of new soil show that this process takes place in stages which follow each other according to a fairly definite sequence. Such a sequence is known as a *succession.* This principle of succession is one of the fundamental conceptions in the modern study of vegetation. It may be studied where land has been freshly exposed, as along the embankments of newly made railway cuttings, or along a sandy sea-coast. One of the most interesting studies in colonisation and succession has been that on Krakatoa, a volcanic island about 20 miles from Java and 50 miles from Sumatra. In 1883 a volcanic eruption destroyed the existing vegetation. The island was visited in 1886, 1897 and 1906. On the first visit it was observed that the soil was being colonised by Blue-green Algae, mosses and ferns, all reproduced by air-borne spores. Along the shores were found seeds and fruits, which had been carried by water currents, and about nine different species of these had germinated. Two of these species of Spermatophyta from the drift zone had spread inland, and were growing with four species of Compositae and two of Gramineae. These last six species had clearly been air-borne. In 1897 there were 62 species of vascular plants of which 50 were Spermatophyta. Estimates of the total immigrant vegetation gave about 60 per cent. carried by ocean currents, 32 per cent. by air, and about 8 per cent. by birds. On the third visit in 1906 the island was almost entirely covered by vegetation. It had become a closed community of individuals competing with each other towards the establishment of the climatic climax vegetation characteristic of that region.

This illustrates a point of considerable importance in vegetational studies, which is that the age of the area studied must be taken into account. The first colonists were the pioneers. Their seeds and spores were transported at least 20 miles by air or ocean currents, and they were able to tolerate the conditions prevailing on the island and so survive. But in consequence of their presence, forming humus, and of weathering of the land surface, the habitat became gradually modified and other plants amongst later arrivals found the modified conditions more congenial to their growth. The pioneers were few and independent of each other; later, the species and the individuals were more numerous and there was competition.

As a result of competition some individuals and even species die out, whilst others multiply. Hence, in the closed stage, the number of species are fewer, but of these one or two may predominate and so control the habitat, whilst the remaining species become subservient to them.

On any freshly exposed land surface we have, then, a *succession* of communities following each other in a definite sequence and *progressing* to a *climax* community dominated by one or more species. If the climax community is destroyed successional colonisation of the site tends to reproduce it in time.

In any normal progression on land each stage in the succession reacts on the habitat so as to enable the succeeding stage to commence. This gradually introduces conditions in which the preceding stage is unable to exist. The last stage before the climax is reached is called the *preclimax*. A succession of communities, each fulfilling a definite rôle in the sequence leading to a climax, is called a *sere*, and if the sere includes all the stages from bare ground to climatic climax, it is called a primary sere or *prisere*.

A prisere is the exception rather than the rule on the earth's surface as we know it, because man has multiplied and spread his influence far and wide. He has either completely replaced the natural vegetation, e.g. forest to grassland, or has modified it to a greater or less extent. If he slackens his activities or completely removes his influence, the vegetation tends to initiate a new process of development towards the natural climax. Such a new sequence, where nature takes over from man or other interfering agency, is called a *subsere*.

As already mentioned, the climatic climax in the moister tropical regions is forest. In some areas this has been destroyed and replaced by grazing and arable land. In some others, the original forest trees and undergrowth have been replaced by trees such as rubber and coconut. If man's influence were removed, much of this land would revert in time to the original forest, but some of it might be unable to do so, owing to the ground having become marshy and waterlogged. Such ground would support hydro- or hygro-phytic vegetation. This is regarded as a *sub-climax* in that it is hindered from progressing to climax by the prevailing edaphic conditions. Biotic factors, e.g. grazing, too, may prevent progression beyond a sub-climax as in the cases of grassland, pasture and, to some extent, heath.

4. Terminology

A community may be studied from the point of view of its place in a succession. Its composition may also be studied, by listing the species which are present, noting their life-form and frequence, observing their relations one to another, and deciding which are dominant, and which subsidiary. Such studies have led to the development of the concept of the *formation*. Tansley defines a plant formation as a unit of vegetation *formed* by habitat and *expressed* by distinctive life-forms. Generally speaking the plant formation corresponds to a climax and is in fairly stable equilibrium, but this is not always the case. Certain stages in a prisere may be regarded as formations when conditioned by a more or less permanent combination of habitat factors with which are correlated definite life-forms.

Within a formation we may distinguish *associations*. Each association is dominated by a different species and may have at least some different associated species. Each is of definite floristic composition usually relateable to certain conditions of habitat. The floristic composition of an association may be classified into species that are (*a*) dominant, (*b*) sub-dominant, (*c*) abundant, (*d*) frequent, (*e*) occasional and (*f*) rare. The dominant species is not necessarily the most abundant, but it controls the development of the subordinate species. The term *consociation* is applied to that part of an association dominated by a single species, after which it is named. Thus a consociation of *Quercus Robur* is named Quercetum Roboris, of *Agropyron junceum*, Agropyretum juncei, etc. If two species are dominant in an association, such as *Quercus Robur* and *Q. petraea*, the name Quercetum Roboris et petraeae is applied to it, and so on.

A further subdivision of an association or consociation is into *societies*. Most societies are due to variations in habitat conditions which permit species differing from those of the association as a whole to become locally dominant. Thus in Quercetum petraeae we may have areas occupied by a dense growth of brambles, that is a *Rubus* society, and similarly, *Pteridium* (bracken), *Scilla* (bluebell), *Mercurialis* (dog's mercury), and other societies.

Within an association, definite *layers* may be recognised. The layering is represented by the differing heights of the component species above ground, and the different depths occupied by their root systems below ground. We speak of the tree layer, shrub layer, and field layer above ground, and in oak woodland in England, for instance, we may have grasses (surface rooted), bracken (deeper), bluebell (still deeper), and trees. The plants may vegetate at different times of the year, also, so that the factors are edaphic and seasonal. The seasonal variations in the appearance of an association are called *aspects*. In British woodlands, again, for example, the first aspect might be wood anemone, followed by bluebell, then grasses, then ferns.

5. Artificial Plant Communities

Ecological studies need not be confined to natural or semi-natural vegetation. The wholly artificial plant communities that abound in this country offer a fruitful field for ecological observation. Even in towns and cities opportunities occur for work of this type.

Successional colonisation may be observed in bare areas (e.g. of demolished buildings, coal-tips, etc.) and the establishment of the pioneers may be related to their method and efficiency of seed dispersal as well as their fitness for the particular habitat. Playing fields provide a means of studying the effect of excessive treading on the vegetation (few plants can persist near the " goals " of a football field), or of liming (when lime is applied to mark out the field). The respective effects of continued grazing and of mowing for hay may be seen in pastures and meadows, whilst on lawns continual mowing does not destroy certain low-growing weeds. In temperate climates the difference in the exposure of the north and south sides of a hedgebank may be reflected in their differing floras. In arable land the crop determines the type of cultivation, and the cultivation in turn largely determines the nature of the weed flora. The flooding of paddy-fields, for instance, prevents the establishment of weeds which are unable to tolerate continued submersion of their roots in water. With some other crops weeds may be few because cultivation operations are frequent when the crop-plants are small, whilst later the crop forms an almost complete leaf-canopy which hinders the establishment of weeds. Footpaths have a flora differing from that of the fields which they cross, due to treading and often to the increased illumination that they receive.

Numerous other examples might be cited, and no student need neglect ecological observation and study for lack of opportunity, for equally in natural, semi-natural, and artificial vegetation the establishment and persistence of the various types of plants is dependent on the environmental factors.

6. Forest

(*a*) RAIN-FOREST. Various forest types are met with in the Indian region. Where the temperature is high and moisture is abundant throughout the year, rain-forest is the dominant type.

Such conditions prevail along the Malabar coast, in the eastern Himalaya, in Burma and in the south-west of Ceylon. In these regions the dry seasons are so short that they have little effect. Tropical rain-forest is characteristically evergreen. In the Indo-Malayan region primary rain-forest is a mixture of different species of trees, but members of the Dipterocarpaceae predominate. As a rule no one species is dominant by itself and it has been suggested that the failure of any one species to gain the upper hand is due to all the species in the mixture having very similar ecological requirements. The trees usually have straight, columnar stems bearing branches in the upper part where the light is more intense (Plate VI). Climbing plants are very numerous. They grow rapidly towards the light and spread out at the tops of the trees, while their twisted woody stems are often looped in festoons from one tree-trunk to another. The number of epiphytes is very large. Some are on the upper branches where the illumination is greater, others clothe the stems lower down. Liverworts and Algae extend even to the surfaces of the leaves. Below the main canopy are smaller trees and shrubs which can tolerate a certain amount of shade. Below these again, herbaceous vegetation occurs. Where the illumination is weak the undergrowth is poorly developed, but in places where sufficient light is able to penetrate, and particularly along the edges of roads and clearings where it can reach the lower levels of the forest from the side, the undergrowth is often very dense.

Tropical rain-forest therefore consists of different associations of plants occupying different layers. Conditions are ideal for plant growth, but only those plants which can reach the upper levels are able to secure full sunlight. Owing to the high elevation of the sun during the middle of the day, light penetrates the leafy canopy to a considerable extent and it is only when the illumination in the lower layers falls below the requirements of extreme shade-loving plants that green vegetation entirely disappears.

(*b*) DRY EVERGREEN FOREST. In parts of India such as the eastern coastal districts of Madras, and parts of the eastern districts of Ceylon, where the total rainfall, although moderate in amount, is reasonably well distributed throughout the year, dry evergreen forests occur. Trees such as *Diospyros ebenum*, *Mimusops hexandra*, *Pterospermum canescens* and others occur here. The average height of the trees is less than in wetter regions and the undergrowth is less dense. Epiphytes are less numerous, but among them are orchids, e.g. *Vanda* spp., which can tolerate a certain degree of drought. Whenever water is available such orchids can absorb it very rapidly by means of the velamen layer which covers the surface of the aerial roots.

(*c*) DECIDUOUS FOREST. As already mentioned, the rainfall in India is largely connected with the monsoons. There is a rainy season during the south-west monsoon, but, in most parts, the north-east monsoon brings little rain so that for about half the year the weather is comparatively dry. In regions where the rainfall is 40 in. or more, but which have a long dry season, deciduous forest is the characteristic type. The trees are more or less leafless during the dry season and resume vigorous growth as soon as the rainy season has commenced. In some areas a good deal of the deciduous forest has been destroyed by the practice of felling and burning the trees and undergrowth, in order that cereal crops may be grown during the rains. The soil, which is at first highly fertile, soon becomes exhausted and then the area is abandoned. A scrubby jungle develops, but if this is left undisturbed, it ultimately reverts to forest.

In may parts of India the occurrence of annual fires is an important factor affecting forest vegetation. Rain-forest, if left undisturbed, is usually too damp to burn, but in some areas its destruction by man's activities makes it possible for fires to occur every year. The effect of these is to encourage the growth of deciduous forest, as the trees comprising it are more resistant to fire than those of the rain-forest. In some regions with a heavy rainfall deciduous forest is prevalent, although it is probable that these areas were formerly covered by evergreen rain-forest. This is indicated by the fact that if the forest is protected from fire, evergreen species tend to appear and to establish themselves at the expense of the deciduous types.

The existence of forest is dependent on rainfall, and as conditions become more arid the forest gradually gives place to thorny scrub with small scattered trees. In the south of India and in the drier parts of Ceylon, thorny species of *Acacia* are prevalent and *Euphorbia antiquorum*, a tree with succulent cladodes, sometimes becomes a conspicuous feature of the landscape (Plate VII, 2). Where the total rainfall is extremely small, as in Sind and the southern Punjab, trees can survive only in the neighbourhood of the rivers.

(*d*) HILL-FORESTS. In the higher mountains of the tropical parts of India and Ceylon the mean temperature is much less than it is in the neighbouring warm low-country. The air becomes cooled as it ascends the hill, but on clear days the sun's rays are powerful and the daily range in temperature and humidity may be considerable. The trees in the hill-forests tend to be less tall and usually have smaller leaves. Tree-ferns are common at higher elevations in sheltered places (Plate VI). Epiphytic orchids are fairly numerous and the branches of the trees are often covered with mosses and lichens. Shrubs belonging to the genus *Strobilanthes* are found in some places in large numbers and many of them show what is known as gregarious flowering. All the plants of one species in a district develop together for a number of years and come into flower at about the same time and then die. The seeds are shed and when they germinate a new crop of plants grows up until it, in turn, reaches maturity.

In Ceylon many of the hill-forests in the moist region were exterminated when coffee was first planted. Later, the coffee, together with further areas of the original forest, was displaced by the planting of tea.

Some parts of the western Himalayan forest region are interesting in showing a well-marked altitudinal zonation of the trees. Above a height of about 3000 ft., broad-leaved trees, characteristic of temperate climates, such as oaks, elms, walnut, poplar, horse-chestnut and others appear, but above 7000 ft. these give place to conifers of various kinds. Different species characterise well-defined altitudinal belts. Above 11,500 ft. the vegetation is alpine, and birch, junipers and rhododendrons occur. In the eastern Himalayan districts the climate is moister and the species which occupy the different altitudinal zones are for the most part different from those which occur in the western Himalaya.

7. Grasslands

Grasslands, which form such a prominent feature of the vegetation of the British Isles, are comparatively rare in the tropical parts of India. In the moist lowlands the competition from trees and shrubs is too great, in the drier parts the conditions are too severe, to favour the establishment and maintenance of extensive areas of grassland. Such grasslands as occur at the lower elevations owe their continued existence to human activity. In areas where the climax vegetation is forest, the destruction of the forest by fire may result in the development of savannas. In these the vegetation consists of tall grasses, principally *Imperata cylindrica*, with scattered trees. The maintenance of the savannas depends on the annual occurrence of fires during the dry season. In spite of these fires, certain fire-resisting species of trees may succeed in establishing themselves among the grass. Of these, the most noteworthy in the sub-Himalayan region is sal (*Shorea robusta*). Although the young stems are burnt down to ground level annually, the root system persists and ultimately is able to give rise to a stem which is sufficiently robust to withstand the fire. In this way the number of trees may gradually increase until their shade is sufficient to kill the grass.

In the hills, especially in the Khasias and the Nilgiris, rolling expanses of grassland may occur. In Ceylon, also, in certain regions at all elevations above 2000 ft. are found the so-called patanas, which are grassy plains and slopes of considerable extent. These have been thoroughly investigated and may be used as an illustration which will apply to similar areas in India. At the higher elevations the rainfall is heavy and is fairly evenly distributed throughout the year. The soil is dark in colour and very rich in humus. Some of the patanas are comparable to the moorlands which are found in temperate climates, although true peat appears to be absent. The vegetation is chiefly composed of grasses, which at the lower elevations grow in a tufted manner, but at higher elevations form a turf. In swampy places above 5000 ft., species belonging to the Cyperaceae and several species of *Eriocaulon* are abundant and in a few places *Sphagnum* is found. Above 5000 ft. also, the flora changes type as compared with that at the lower elevations, becoming much more like the European flora in its composition, including species of *Anemone*, *Thalictrum*, *Ranunculus*, *Berberis*, *Hypericum*, *Rubus*, *Potentilla*, *Alchemilla*, *Agrimonia*, *Valeriana*, *Dipsacus*, *Campanula*, *Gentiana* and many others.

In the higher regions in some areas the hill-tops are occupied by forest, the patanas occupying the lower slopes and the valleys. The boundary separating the grassy vegetation from the forest is extraordinarily sharp, the intermediate zone being often only a few feet wide. In this zone the plants consist mainly of stunted forest trees and of shrubs such as occur in the patanas, together with a few grasses. The boundary is not in any way related to the physical features of the land. Small areas of forest extend here and there into the patanas and small areas of patana can be found completely enclosed by forest. Of the many different trees which are found in the high-level forests, only one species, *Rhododendron arboreum* (Plate VII, 1), is able to establish itself among the grasses of the patanas.

On the eastern side of the mountain ridge in Ceylon, between 2000 and 4500 ft., are patana grasslands of a different type. Except during the period of the north-east monsoon, the rainfall in these regions is scanty. Owing to denudation the soil is shallow and the flora consists chiefly of coarse, wiry grasses. The patches of forest, in contrast to what occurs at higher elevations, tend to be confined to the depressions where soil accumulates and more water is available. Recurrent grass fires, together with the poverty of the soil of the patanas, prevent the forest from extending and probably the present areas of forest and patana have existed, with little change, for a very long time.

8. Vegetation of Ponds and Lakes

The character and extent of the plant population of ponds and lakes are governed by such factors as supply of oxygen, carbon dioxide, and mineral salts, nature of substratum, depth of water, light intensity and temperature.

Not only does light intensity vary in proportion to the depth of the water, but it is dependent on physiographic features. The shade cast by high, steep banks affects the amount of light reaching the water, and also its temperature. Shallow water tends to be warmer in summer than deep water. Streams flowing over hard rock do not provide the amount or type of silt required for the support of many aquatic plants. Rooted aquatics make use of the nutrient ions present in the substratum more than of those present in the surrounding water. Lack of bases in the water prevents the decomposition of humus, and this tends to accumulate. On the other hand, where bases are in good supply the silts contain broken down humus.

It will be readily seen that such considerations will be reflected in the type of vegetation inhabiting any given lake or pond, and, in fact, also in the fauna. Preponderance of desmids or diatoms is governed by the operation of these factors, and similarly the species of higher plants, whether submerged (e.g. *Nitella*, *Hydrilla*, *Utricularia*, *Blyxa*, *Ceratophyllum*), or with floating leaves (e.g. *Limnanthemum*, *Nymphaea*, *Nelumbium*), or with shoots partly under water and partly aerial (e.g. *Ceratopteris*, *Monochoria*, *Lagenandra*, sedges, rushes, grasses). These plants show great variety of life form. The pioneer vegetation consists of submerged plants which by their remains and by accumulating silt, raise the level of the substratum and permit colonisation by plants with floating leaves, then plants of the reed swamp, and, finally, where the substratum level reaches water level, fen and marsh.

In the plains of India, owing to the well-marked division of the year into a dry season of considerable duration and a wet season which is comparatively short, bog and marsh plants are rare. During the fierce heats of the dry season, everything resembling a marsh is liable to become dried up at a very early period, and only in a very few places do such stations for plants remain marshy throughout the year. In the hills, where the country does not dry up to so great an extent in the dry season, many genera of marsh plants which occur also in Europe may be found, especially in the north, but in the plains only a few plants are to be seen belonging to this group. These include a good many of the Cyperaceae, especially *Carex, Cyperus, Eleocharis, Scirpus, Fimbristylis*, a few grasses, rushes (*Juncus*) and others. In the rice fields there grows a special flora of small annuals which die when the fields are drained for the harvest.

Among the higher plants which are found in ponds and lakes, there are also those which float freely on the surface of the water, e.g. *Azolla, Salvinia, Lemna* and larger plants such as *Pistia stratiotes* and *Eichornia crassipes*. The latter floats high on the surface of the water. It is a South American plant. In Ceylon, where it was introduced, it spread very rapidly and became a serious pest.

An extremely interesting case of adaptation to specialised aquatic life is found in the Podostemonaceae, a family of tropical flowering plants which occurs both in India and Ceylon. Members of this family grow attached to rocks in swiftly running water. The plant-body is a thallus-like structure, derived usually from an adventitious root, and differs from that of most water plants in the absence of intercellular spaces. It is attached to the rocks by special holdfasts and gives rise to secondary shoots which bear leaves and flowers. The flowers open when the level of the water falls. The seeds are shed on the rocks during the dry season and germinate after the rains have come and the water has risen.

9. Vegetation of the Seashore

(*a*) MUD FLATS, SALT MARSH. Extensive areas of sea coast in the sheltered estuaries of rivers are subject to periodic inundation by the tides. The substratum is a mixture of sand and mud in varying proportion, depending on the nature of the ground drained by the river. The detritus brought down by the river is deposited at its mouth if the coast is free from tidal erosion and the scour of ocean currents. On such a substratum, a characteristic vegetation is developed of plants which can tolerate varying degrees of immersion in salt water, and a relatively high percentage of common salt in the soil. These plants are called ***halophytes***.

In the tropics the mud banks in sheltered positions in the swampy estuaries of tidal rivers or along the margins of coastal lagoons are often occupied by **mangrove**. This is a characteristic woodland formation which is found as a rule in places where the mud is left actually bare during a portion of the day, but is subject to periodic immersion in water which is definitely salt or brackish. Although the plants which occur in the mangrove vegetation belong to several different families, they show many points of similarity which may be regarded as adaptations to their mode of life. In the Eastern mangrove, the chief genera are *Rhizophora* and *Bruguiera* (Rhizophoraceae), *Avicennia* (Verbenaceae), *Sonneratia* (Sonneratiaceae) and *Aegiceras* (Myrsinaceae). Of the Asiatic species, *Rhizophora mucronata* is particularly well adapted for colonising soft mud and for resisting the flow of the tide. The short stem is supported on numerous downwardly-curving adventitious roots, and as the tree develops other roots grow down from the branches (Plate VIII, 2). In many of the other genera of the mangrove vegetation the stem is anchored to the mud by horizontal roots growing below the surface. Such roots are covered continuously by water or wet mud and hence are growing in surroundings deficient in oxygen. Oxygen can only reach the tissues by diffusion from above through the intercellular spaces, and in several genera this process is aided by special arrangements. In *Sonneratia* and *Avicennia* negatively geotropic roots arise as branches on the main subterranean roots. These branches grow straight up into the air above the surface of the mud. They are called *pneumatophores*. They possess lenticels and large intercellular spaces. *Bruguiera* has a somewhat different arrangement. Horizontal roots as they grow come above the surface of the mud and then bend down again. At the tops of the knee-like portions numerous lenticels are developed. In *Rhizophora* the exposed parts of the adventitious roots have lenticels through which oxygen can enter.

A characteristic feature of many mangrove genera is what is called *viviparous germination*. The seeds germinate within the fruit while this is still attached to the tree. In *Rhizophora* the hypocotyl elongates to a length of 20-40 cm. or even more, and pushes the radicle out through the pericarp. Finally the hypocotyl and plumule become detached from the cotyledons, which remain in the fruit. The seedling falls like a dart, and if the tide is low, the pointed end of the radicle may become stuck in the mud. Lateral roots soon grow out and the young plant becomes firmly attached. If, however, the seedling falls into deep water it floats vertically and if, later, it comes into shallow water, the radicle has a good chance of becoming fixed in the mud. The successful colonisation of mudbanks by *Rhizophora* may be due largely to this method of germination. A possible additional advantage is that it eliminates the necessity of the seeds having to germinate in salt water. However, as viviparous germination is absent in some mangrove genera, e.g. *Sonneratia*, its occurrence does not appear to be essential in all cases.

In lagoons and rivers where the tidal rise and fall are still considerable, but where the water is less saline, the mud is sometimes colonised by the Nipa Palm. This is frequent in the Sunderbuns, in Malaya and on the south-west coast of Ceylon. It forms a local association in which members of the Rhizophoraceae are usually absent, but which may contain *Avicennia officinalis* and *Sonneratia acida*.

Apart from the mangrove vegetation, other halophytes are found on mud flats or salt marshes subject to periodic immersion by salt water. Among these are *Salicornia brachiata* and *Arthrocnemum indicum*. Both have fleshy jointed stems and are apparently leafless. Several species of *Suaeda* grow on the mud in tidal swamps. These are shrubby plants with fleshy leaves.

(*b*) SAND-DUNES. Sand-dunes are built up by the accumulation of blown-sand. They are a feature of parts of the coast, but they may occur in inland, desert regions of continental areas, too. Coastal sand-dunes are gradually built up from drifting sand. On the flatter parts of the coast the receding tide exposes expanses of sand. The surface dries and an inshore wind carries the surface particles inland. Any obstacle in their path causes particles to be deposited and an embryo dune to be formed. The obstacles may be fragments of seaweed, or articles deposited by the receding tide. Particularly in the drift-zone of the highest spring tides, left more or less undisturbed by succeeding tides, seeds and fruits which have arrived there through some mode of dispersal, germinate, and many of the seedling plants become established. The plants of this littoral zone which survive are those able to tolerate such conditions as exposure to moving sand, high winds, high day temperatures, some salt, e.g. from spray, and, by their growth, to keep pace with the constant accumulation of sand which would otherwise bury them.

Of the plants which grow on sandy shores just above the reach of the waves, one of the most widespread in the tropics of both the Old World and the New World is *Ipomoea pes-caprae*. This has bilobed leaves and purple bell-shaped flowers. The long creeping stems grow along the sand, giving off adventitious roots at the nodes. The surface of the sand is thus covered and held firm and is less likely to be disturbed by the wind. Another plant which occurs in the Indian region, *Spinifex littoreus*, is often associated with *Ipomoea pes-caprae* (Plate VIII, 1), or forms a consociation of its own. *Spinifex* is a grass with stout, creeping stems, more or less buried in the sand and giving off tufts of leaves and adventitious roots at the nodes. The female spikelets have long spiny bracts and are massed together to form a spherical head, which breaks off when the fruits are ripe and is rolled along the beach by the wind. Finally, it becomes embedded in the sand, where it soon breaks up and liberates the seeds. *Spinifex* is admirably suited to the special conditions under which it grows and plays an important part on tropical coasts in the building of dunes.

Among other tropical plants which help to bind the sand are the sedge *Remirea maritima*, and a Leguminous plant *Canavalia podocarpa*, which grows in a similar manner to *Ipomoea pes-caprae*, but may be distinguished at once by its trifoliate leaves.

(*c*) BEACH-JUNGLE. Above high-tide level the sand is stabilised by the growth of creeping species, and on tropical beaches, a little way back from the sandy shore, there is often a characteristic formation of trees and shrubs. The most striking members of this formation are species of *Pandanus*, the so-called screw-pines. These are trees with large, narrow, spirally-arranged leaves. The branched stems bear numerous thick adventitious roots which anchor the plants firmly to the sandy soil. Among the tangle of roots, fallen leaves and other organic material become enmeshed and by their decay serve to enrich the soil. The screw-pines appear to be particularly well adapted to withstand the exposed conditions of the seashore. Among them, or on the sheltered side of them, other trees and shrubs are found. These mostly show xeromorphic characters such as succulent stems and leaves, thick leathery leaves, or hairiness in the younger parts. In many of the moister tropical regions, the beach-jungle has been replaced by plantations of coconut (*Cocos nucifera*), which grows particularly well in such situations.

The trees and shrubs of the beach-jungle very often have fruits which can float in the sea for long distances without injurious effects from the salt water. Fruits of *Cocos*, *Pandanus*, *Barringtonia* and many others are commonly found washed up on the seashore. In this way these plants have become widely distributed. The best known example is the coconut palm which has thus established itself on newly formed coral islands.

The student must realise that the preceding account of plant communities is incomplete. It is intended merely as a guide to problems with which the ecologist is concerned, and the serious student should read the works of reference on this subject.

CHAPTER XXII

GENETICS, HEREDITY AND EVOLUTION

1. Heredity

The resemblance that exists between parents and their offspring is epitomised in the statement, " Like begets like." This resemblance is due to the fact that the offspring inherit certain characteristics from their parents. The scientific study of inheritance constitutes Genetics.

Recent advances in our knowledge of this branch of Biology owe much to Cytology. Increased knowledge of the details of cell, and particularly of nuclear, structure throw much light on the mechanism of inheritance.

Although offspring resemble their parents, they are rarely identical with them. They show considerable variation. This will be seen clearly if some particular character capable of measurement is considered. If, for instance, we save all the seeds from a single plant of the scarlet runner bean and sow them, all the resulting plants will be similar and clearly recognisable as scarlet runner beans. Between individual plants small but discernible differences in height, length of pod, etc., exist. These differences are, in part, but only in part, due to differences in the environment of the plants, and the features exhibited by any particular plant result from the interplay of inheritance and the effect of the environment. Not all the differences between individuals are due to environmental effects. Some of the individual variations occur because all the offspring of the same parent do not inherit exactly identical characters.

Individual variations can be subjected to statistical analysis, and this mathematical study of variation constitutes Biometry.

2. Biometrical Study of Variation

This has been applied to variation in those characters that can be readily measured. In the simplest cases the method consists of, for example, the measurement of a given character in a large number of individuals. The measurements are then arranged from the lowest to the highest in ascending order of sequence, and the number of individuals counted for each measurement. The result can be represented graphically.

Suppose we measure the length of the lowest fruit in a large number of plants of evening primrose (*Oenothera biennis*). The range of measurements ascends from 15 to 34 mm. We decide to arrange the individual fruits measured in 20 classes, the first 15 mm., next 16 mm., and so on up to 34 mm., then we count the number in each class. This number is the frequency for each particular class. Using squared paper we number the squares along the abscissa according to our classes, 15 to 34, and along the ordinate the various frequencies obtained. We then complete the curve. Fig. 407 represents such a graph. In this case the curve approximates to an ideal curve which is called the normal curve of variability. The longest ordinate indicates the measurement of greatest

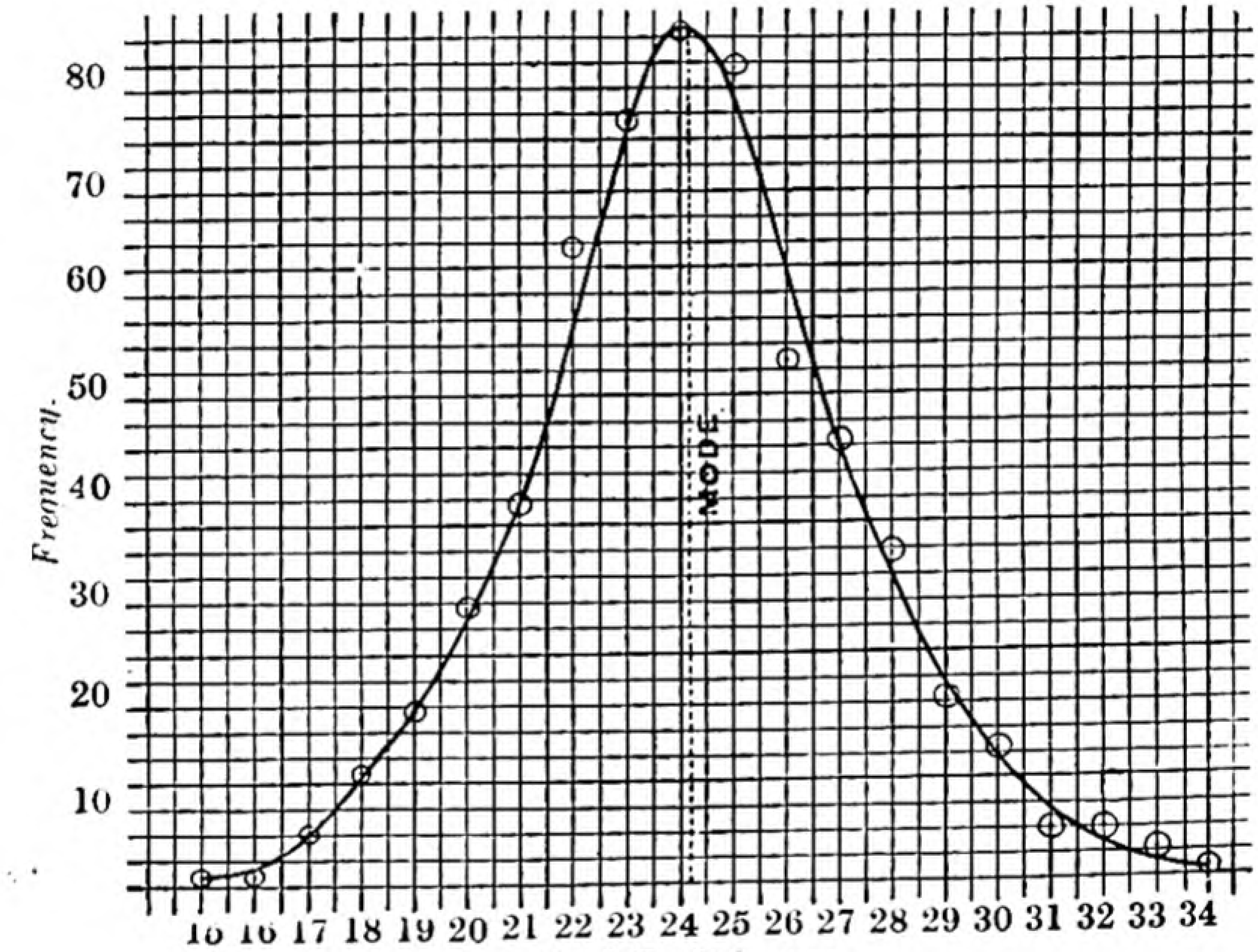

Fig. 407.

The points indicate the actual frequencies obtained; the curve as drawn amongst the points may be taken to represent approximately the normal curve of variability.

frequency and is known as the modal value. In this figure it is approximately 24·2.

The form of the curve will indicate the nature of the variation. If there is a wide range of variation the curve will tend to be wide; if there is a narrow range, the curve (with equivalent scale of representation) will be narrow and steep.

The variability curve obtained may not be quite symmetrical about the modal ordinate. In this case it is said to be *skew*, and the modal value will depart more or less widely from the mean or average of the measurements. The amount of skewness varies. In extreme cases the curve may be all on one side of the longest ordinate.

Biometricians maintain that by statistical study, repeated at intervals on different generations, of the variability in a population (*i.e.* any assemblage of organisms of the same species in a particular area) it is possible to determine, by observation of the differences that have occurred, whether natural selection has been acting and, if so, in what particular direction. In this connexion it should be noted that occasionally graphs with two (or more) humps, more or less distinct, *i.e.* with two (or more) frequency maxima, are obtained.

3. Johannsen's Pure Line Theory (1903)

Johannsen, Professor of Botany at Copenhagen, experimented with kidney beans and other plants, and arrived at conclusions which have an important bearing on questions of variation and heredity. He defined a *pure line* as consisting of all the descendants of a single individual by continued self-fertilisation. This means that the offspring in each generation have one parent only, and there is no mixing of different germ-plasms from two parents.

He took a number of seeds from nineteen bean plants. With regard to seed weight they showed normal variability, and he determined the mean or average seed weight of the population. He sowed the different lots *separately* and thus separated the population into nineteen pure lines. He found in each pure line that, while there was nearly normal variability of wide range, there was a *distinctive* mean weight of seed.

Further, on arranging seeds *of any one of the pure lines* in classes according to weight, sowing these separately, and determining the mean weight of seeds produced by each set of offspring, he found *in all cases* that it approximated to the mean seed weight of the pure line from which the classes of seeds were taken. This means that the variation in seed weight within each pure line had not been inherited; within a pure line selection has no effect. The explanation of this seems to be that the normal variations in a pure line are not inherited variations, but are of the nature of modifications due to environmental influences. The same explanation would be given of the normal " variation " in the development of a single character in *one* individual, e.g. seed weight, number of lateral veins in the leaves, etc. It is to " variations " of this kind that the term " fluctuations " is more strictly applied.

Johannsen found, however, that *in a population*, which may be regarded as consisting of a large number of pure lines of different type, selection was effective up to a certain point. The explanation seems to be that selection results in the separation of the pure line which, with respect to the character selected, shows greatest deviation from the mean of the population.

4. Natural Selection

We have seen that individual variations are not inherited, but that when dealing with a mixed population (*i.e.* not a pure line) it is possible by artificial selection to obtain pure lines exhibiting a particular character to a marked degree (e.g. heavy or light seeds in the kidney bean). In nature, natural selection is operative. Amongst all the offspring of a single parent variations exist and seed is generally produced so abundantly that it would be impossible for all the resulting seedlings to become established and to grow into adult plants. Of the seedlings that result from the germination of the seed the majority will fail to reach the adult stage. In the "struggle for existence" only the "strongest" will survive. "Strength" or "vigour" may be due to a favourable environment, or to inherited characters, or to both. If natural selection operates on innumerable successive generations, it is easy to imagine that each succeeding generation will be slightly more vigorous, or more resistant to adverse conditions, than its predecessor. By this method, in the course of time, a race of plants might arise that was very different from its ancestors, and Darwin suggested that it is in this way that new species arise. It is unlikely, however, that natural selection would be more efficient than artificial selection, and we have seen how the latter can select a pure line from a mixed population, but cannot go beyond this point.

5. Inheritance of Acquired Characters

The power of responding to environmental influences is possessed by all organisms. Many plants possess the power of accommodating themselves to their environment to a marked degree, and exhibit characters that have been induced by the factors that constitute the environment of the plant. For instance, the leaves of the beech tree respond to insolation, so that on the sunny side of the tree the leaves possess two layers of palisade cells; whereas one layer only is present in leaves that have been shaded. Characters induced in the plant in this manner are spoken of as modifications or acquired characters, and the question arises as to whether or not they are inherited. Characters acquired during the development of the individual reappear in the offspring, and the offspring grow under precisely those conditions that induced the appearance of the character in the parent. This is not necessarily because the characters have been inherited. They may be, and certainly in most cases have been, acquired by the offspring in exactly the same way that they were acquired by the parent.

Many biologists, however, believe that modifications induced by environment are inherited and reappear in the offspring even in the absence of the particular conditions that induced their development in the parent. One of the principal exponents of this view was Lamarck. The inheritance of acquired characters would offer a ready explanation of many of the marked adaptations to environment exhibited by many plants in their wild state, and which persist in their offspring. Experiments that have been devised to prove the inheritance of acquired characters have yielded negative results, and we have no knowledge of any mechanism by which such characters could be inherited.

Sometimes the operation of external factors does result in the production of offspring that differ widely from their parents. When, for instance, the immature reproductive organs of some plants are subjected to X-radiation, they produce seed which gives rise to plants that differ markedly from their parents. Further, the " new " characters produced in this way are inherited. We are here dealing with artificially-produced mutations (§ 6). They are produced because the X-rays have induced changes in the " germ plasm " of the plant. Many examples of this are known, and their existence must not confuse the student's understanding of the problem of the inheritance of acquired characters. Inheritance of acquired characters supposes that modifications induced by environment in the vegetative parts of the plant can in some way influence the nuclear structure of the cells concerned with reproduction. As previously stated, however, experimental evidence in support of such a view is lacking.

6. Mutations (Discontinuous Variations)

We have seen how members of a species, or the offspring of a single parent, exhibit variations in one or more characters. The members, however, can usually be arranged so as to form a continuous series grading almost imperceptibly between two extremes.

Discontinuous variations cannot be arranged in this way. They are more or less sharply marked, abrupt or sudden deviations from the type exhibited by the species. To the very marked or extreme forms of such variations the names "sports," " breaks," " monstrosities," have been applied. They may all be included under the general term **mutations.** The individual showing the mutation is now called a ***mutant.***

Examples of mutation in plants are found in the sudden appearance of forms with cut or laciniated leaves or petals, of double flowers, of differently

coloured flowers, of dwarf forms, of weeping varieties of trees, of red-leaved forms, or hairless varieties. It is believed also that many at least of our varieties of cultivated plants have arisen in this way.

The recognition of the importance and frequent occurrence of discontinuous variations was chiefly due to Bateson. Hugo de Vries of Amsterdam carried out a large amount of work on the experimental side. He cultivated thousands of seedlings of different plants in the hope of recognising such variations. He succeeded in finding a plant, *Oenothera Lamarckiana*, which was producing numerous mutations and some at least of the mutants bred true. He had, in fact, found a plant which seemed to be throwing off new species by mutation.

There was thus a presumption that the characters which distinguish natural species had originated in the same way, and the impression that mutations were variations of the utmost importance in evolution gained ground. This view was strengthened by the discovery of Mendel's work in 1900, for the Mendelian unit characters appeared to be of the same nature as the characters distinguishing species and they were shown to be subject to perfectly definite laws of inheritance. The doctrine of the origin of new species by mutation was enunciated in the Mutation Theory of de Vries (1901-3). According to this theory, new species arise, not by the continuous action of natural selection on small individual variations, but at one step by abrupt or sharply marked mutations.

Mutations, it will be clear, do not arise only when plants are propagated by seed. " Sports " sometimes arise in which only a single shoot of a tree appears to have undergone a change, and such mutations in many cases persist only if they are propagated vegetatively.

7. Hybridisation

Experiments in hybridisation, especially with forms not too widely different from each other, would appear to offer hope of solving some of the problems of heredity. The term hybrid is commonly applied to the offspring of two individuals which differ more or less distinctly from each other in one or more characters. This indeed was its original significance, although afterwards it came to be restricted to the offspring produced by the crossing of individuals of distinct species. Cases are known of hybrids produced by crossing distinct genera.

In the process of hybridisation in Flowering Plants the young undeveloped anthers are removed by means of forceps from one or more flowers of one plant, A, and on the stigmas, when they are mature, is placed pollen from the other plant, B. The flowers to be pollinated must, of course, be protected from access of other pollen, e.g. by parchment bags. With a few exceptions it makes no difference whether A pollinates B or B pollinates A. The hybrid embryos are in the seeds produced in the ovaries of the flowers artificially pollinated.

The results obtained by the many hybridists before Darwin's *Origin of Species* appeared were very conflicting, and contributed little of value to the elucidation of the problems of heredity and variation. The hybrids might be more or less intermediate in character between the parents, or they might resemble one parent in some characters, and the other parent in others. The offspring of hybrid plants in succeeding generations often showed an extraordinary variety of forms, and hence it was usually believed that hybridisation gave rise to great variability. In many cases it was found that the hybrids showed a distinct increase in vigour as compared with the parental forms; a satisfactory explanation of this is still lacking. Finally, hybrids produced by crossing distinct species were usually more or less sterile. Mendel found the true method of experiment, but his work was lost sight of for thirty-five years.

8. Mendel and His Work

Gregor Johann Mendel (1822-1884) was a monk in the Monastery of Brünn in Bohemia; he became Abbot in 1868. His most important experiments were made in the garden of the monastery from 1857 to 1865. The results were communicated to the Natural History Society of Brünn in 1865, and published in the *Proceedings* in 1866. In 1900 they were rediscovered independently by three botanists—Hugo de Vries, Tschermak, and Correns.

Mendel's methods and experiments provided the foundation for genetic research. He used certain varieties of pea, mostly of the edible pea (*Pisum sativum*). His success was largely due to his attending to the following points: (*a*) he was careful to work with pure homogeneous material—the varieties of pea were pure or bred true; (*b*) he considered each character separately; (*c*) he recorded the offspring of each individual separately; (*d*) he kept records up to at least the third generation. The advantages of using varieties of pea for experiment were that they showed constant, readily recognisable differentiating characters, the flowers were regularly self-pollinated and the hybrids perfectly fertile.

Mendel fixed on a number of pairs of sharply differentiated characters by which his varieties of pea were distinguished—yellow or green cotyledons, smooth or wrinkled seeds, tall or dwarf habit (long or short stems), etc. He considered each pair separately.

He crossed a pure tall variety with a pure dwarf variety, and found that *all the hybrid offspring*, constituting what is now called the first filial or F_1 generation, *were tall*, and thus resembled the tall parent. The tall character, or character of tallness, therefore, he called the *dominant character*. He allowed these tall hybrid plants to fertilise themselves, and kept careful record of all the offspring, constituting what is now called the second filial or F_2 generation. He found they consisted of talls and dwarfs in the ratio 3 : 1 (actual numbers obtained were 787 : 277).

The character of dwarfness, therefore, had been latent or unexpressed in the first or hybrid generation; Mendel called it the *recessive character*. He found that if these dwarf plants, forming one-quarter of the second generation, were allowed to fertilise themselves they produced only dwarfs, *i.e.* they bred true and were pure for the dwarf character (*pure recessives*). When, however, the tall plants of the second generation were allowed to fertilise themselves, he found that while one-third of them (constituting one-quarter of the whole second generation) produced tall offspring only and were *pure dominants*, the remaining two-thirds (constituting one-half of the whole second generation) were *impure dominants* or hybrids, resembling the hybrid plants of the first generation, and, like them, producing tall and dwarf offspring in the ratio 3 : 1. Thus, in the second or F_2 generation, *pure dominants*, *hybrids* (or impure dominants) and *pure recessives* are found in the ratio 1 : 2 : 1.

This can be represented graphically as in Fig. 408. The crossing of the two forms is represented by DD × dd, DD being the pure dominant, dd the pure recessive and Dd the hybrid. F_1, F_2, etc., represent the various filial generations.

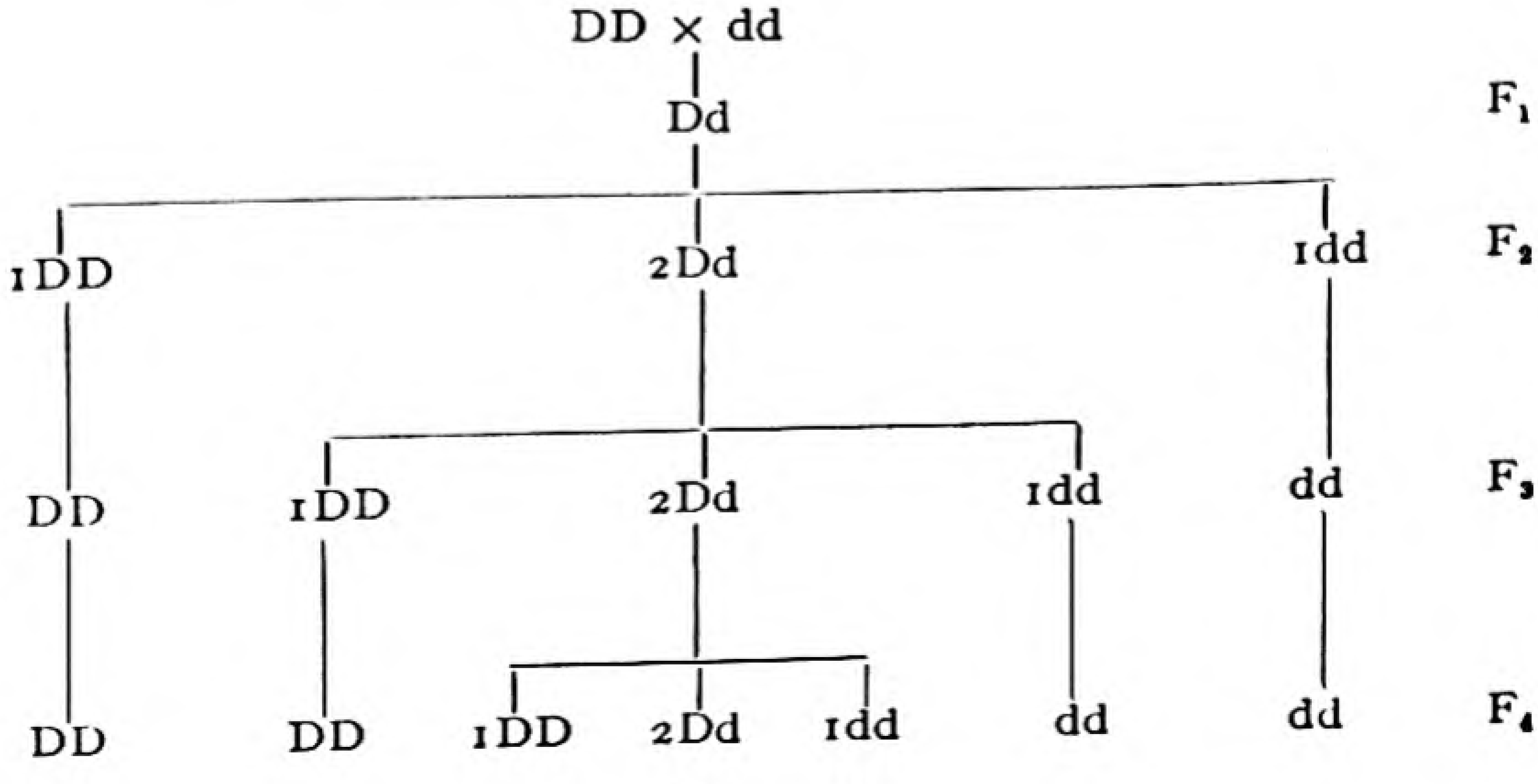

Fig. 408.

The most remarkable feature is the segregation or separating out, in a definite ratio, of pure types from the hybrid in the second and succeeding generations. An explanation of this was given by Mendel. It was that the "germ-cells" (pollen-grains and egg-cells, according to Mendel) produced by the hybrids were separated off or segregated into two equal groups, half of the male and female cells bearing the dominant character (or factor), and the other half bearing the recessive factor.

It is evident that in self-fertilisation the chances of a dominant or a recessive ♂ cell meeting with a dominant or recessive ♀ cell are equal, and the possible combinations in the zygote are thus, as indicated by the arrows in Fig. 409, DD, Dd, dD, dd, *i.e.* DD, 2Dd, dd, which agrees with the experimental result. If we represent dominant and recessive factors by A and *a* respectively, then the expansion of (A+*a*) (A+*a*), *i.e.* AA+2A*a*+*aa*, gives the distribution of pure and hybrid offspring in the second generation.

The chief results of Mendel's work may be stated thus:

(*a*) The idea or conception of pairs of alternative unit characters represented by factors in the germ-cells.

They are called unit characters because they (or, rather, the factors representing them) are inherited as units, *i.e.* they are either inherited or not inherited, they cannot be partly inherited.

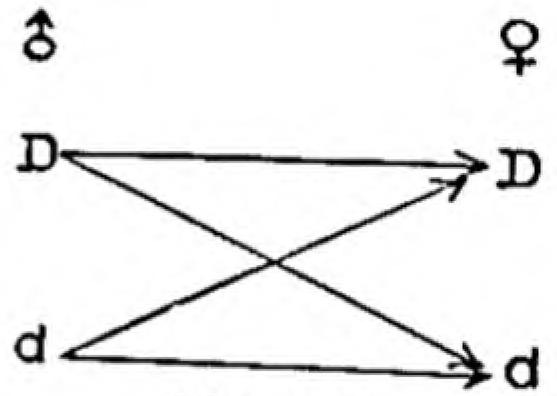

Fig. 409.

(*b*) The idea of dominant and recessive characters. This has sometimes been called the Law of Dominance, but many cases are now known where the hybrid offspring has a character more or less intermediate between the two differentiating characters of the parents. In this case the two pure forms and the ratio 1 : 2 : 1 are distinctly recognisable in the second generation F_2.

(*c*) The separation or splitting off of pure forms from hybrids in the second and succeeding generations.

(*d*) The segregation of factors in the germ-cells. This is the essential part of what is called Mendel's Law.

9. Allelomorphs, etc.

The pairs of differentiating characters are now called *allelomorphs*, of which one in each pair may be dominant, the other recessive. If the dominant and recessive factors in the germ-cells are represented by A and *a* (or B and *b*, C and *c*, etc.) respectively, then the germ-plasm of the zygote and body-cells of a pure dominant will contain the two factors AA, that of a pure recessive *aa*, that of a hybrid A*a*. It is only in the germ-plasm of the zygote and body-cells of the hybrid that the two factors A and *a* are associated. The meaning of the term zygote is extended from the cell resulting from fertilisation to include the organism developed from it. Pure dominants and recessives, therefore, are called **homozygotes** (represented by AA and *aa*), while a hybrid is called a **heterozygote** (represented by A*a*).

The pure dominant is said to be *homozygous* for the character represented by A, the pure recessive homozygous for the character represented by *a*. Each germ-cell of a pure dominant receives a single factor A; of a pure recessive a single factor *a*; but in a hybrid the factors A and *a* are separated and pass into different germ-cells. This is in agreement with the cytologically observed fact of the reduction of the chromosomes in the formation (in the higher plants) of the spores from which the ♂ and ♀ cells are derived. It has to be carefully observed that *germ-cells are always pure*—they never contain both factors of a pair.

10. Two-Character Inheritance

Mendel also carried out experiments with two pairs of differentiating characters. He crossed a variety of pea with *yellow* cotyledons and *round* seeds (both dominant characters) and one with *green* cotyledons and *wrinkled* seeds (both recessive characters). He found that with regard to inheritance these pairs of characters were independent of each other. The seeds obtained were all yellow and round, and, therefore, *since these characters depend on the characters of the hybrid embryos in the seeds*, we may say that the hybrids showed both dominant characters. The seeds obtained from the self-fertilised hybrid plants belonged to four types: (*a*) yellow and round, (*b*) yellow and wrinkled, (*c*) round and green, (*d*) wrinkled and green, in the ratio, approximately, 9 : 3 : 3 : 1 —the actual numbers were 315 : 101 : 108 : 32. The groups, however, are not homogeneous, as Mendel showed by continuing the experiment to the next generation. The results arrived at are best displayed by a theoretical explanation; theory and experiment are in close accord.

If we represent the two pure forms crossed by AABB and *aabb* (A yellow, B round, *a* green, *b* wrinkled), the offspring forming the first or hybrid generation F_1 will be represented by A*a*B*b* and show both dominant characters. The hybrid germ-cells on segregation will be in equal numbers of the four types AB, A*b*, *a*B, *ab* (these are all the possible combinations of the factors—A*a* and B*b* will not occur). In fertilisation any one of four male cells of these types will fuse with any one of four corresponding female cells, and hence there will be sixteen possible combinations, some, however, being identical. These combinations are quite easily worked out; they are also given by expanding

$$(\mathrm{AA} + 2\mathrm{A}a + aa) \times (\mathrm{BB} + 2\mathrm{B}b + bb).$$

They are:—

POLLEN.

		AB	A*b*	*a*B	*ab*
OVULES	AB	AB AB	AB A*b*	AB *a*B	AB *ab*
	A*b*	A*b* AB	A*b* A*b*	A*b* *a*B	A*b* *ab*
	*a*B	*a*B AB	*a*B A*b*	*a*B *a*B	*a*B *ab*
	ab	*ab* AB	*ab* A*b*	*ab* *a*B	*ab* *ab*

Fig. 410.

These sixteen combinations may be grouped together as follows:—

(1) 1 AA BB—homozygous for both A and B (pure type) (2) 2 AA B*b*—homozygous for A only (3) 2 A*a* BB—homozygous for B only (4) 4 A*a* B*b*—heterozygous for both characters	these 9 forms have both A and B — hence all yellow and round.
(5) 1 AA *bb*—homozygous for both A and *b* (pure type) (6) 2 A*a* *bb*—homozygous for *b* only	these 3 have A and *bb*—hence all yellow and wrinkled.
(7) 1 *aa* BB—homozygous for both *a* and B (pure type) (8) 2 *aa* B*b*—homozygous for *a* only	these 3 have B and *aa*—hence all round and green.
(9) 1 *aa* *bb*—homozygous for both *a* and *b* (pure type)	1 wrinkled and green.

The table clearly shows what types are included in the groups forming the 9 : 3 : 3 : 1 ratio of the second generation. The following points should be carefully noted: (1) how complicated is the experimental work in connexion with even two pairs of characters: (2) only four in sixteen offspring are homozygous or pure for two characters; the others are heterozygous with respect to, at least, one pair of characters, and there will, therefore, be further segregation in succeeding generations: (3) in addition to the two pure parental types, two other pure types, AA*bb* and *aa*BB, representing new combinations of the characters, separate out; it is believed that this indicates one way in which new varieties or species may arise; it is also of great practical importance, as it enables new varieties of crop plants to be produced. In this way varieties of wheat which yield flours of high baking quality, and which are also disease-resistant have been synthesised.

11. The Mechanism of Inheritance

Although Mendel, as a result of his experiments and observations, established certain principles of inheritance, he was ignorant of the precise way in which characters are transmitted from parent to offspring. It is now believed that the heritable characters of the plant are localised in the chromosomes as genes. Hence in the nucleus of a tall pea which is diploid, and so has a $2n$ complement of chromosomes, we have in each of two of the chromosomes a gene for tallness; in a dwarf pea a gene for dwarfness, and so on. It is now customary to speak of, say, a gene for tallness rather than a factor for tallness. If the heritable characters of a plant are located in the genes in this way, then mitosis ensures that daughter cells will be provided with all the genes possessed by the mother-cell from which they have been derived. Hence we should expect plants produced vegetatively to be identical with their parents, as they possess the same complement of genes, and we do in fact find that this is so.

When reproduction takes place sexually, the position is different. At some stage preceding gamete-formation meiosis takes place. In Flowering Plants this occurs in the formation of megaspores (embryo-sacs) and microspores (pollen-grains), so that these reproductive cells contain only half the number of chromosomes possessed by the vegetative cells of the parent plant, and by the spore-mother-cells from which they have been derived. Since the spore-mother-cells are diploid, they possess the $2n$ number of chromosomes and hence a double set of genes. The spores, as a result of meiosis possess the n number of chromosomes and therefore only one full set of genes. Thus in the vegetative cells and also in the spore-mother-cells of, say, pure tall peas, we shall have one pair of chromosomes, each member of the pair with a gene for tallness. Pollen-grains and embryo-sacs resulting from meiosis will, however, only possess one chromosome with a tall gene. Hence the generative nuclei of the pollen-grains, and the nuclei of the oospheres (male and female gametes respectively) will each possess only one gene for tallness. When hybridisation takes place between pure talls and pure dwarfs, therefore, male gametes possessing the gene for tallness (T) will unite with female gametes possessing the gene for dwarfness (t), and, similarly, male gametes (t) with female gametes (T).

We can now apply our knowledge of nuclear structure and nuclear division to Fig. 408 and rewrite it (Fig. 411). Pure tall pea plants will have diploid nuclei possessing two genes for tallness (TT). Pure dwarf pea plants are usually represented (tt) since dwarfness is recessive.

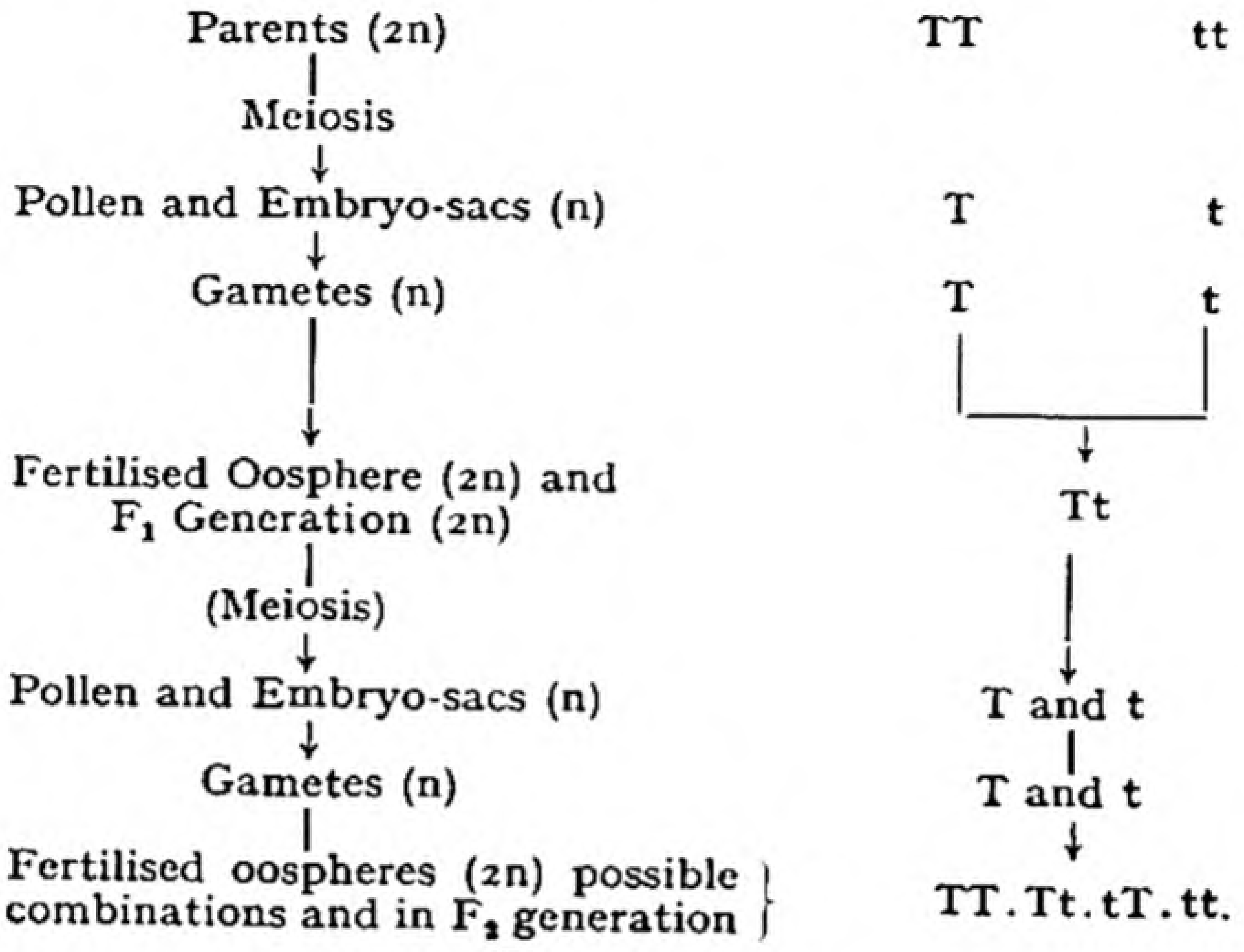
Parents (2n)
Meiosis
Pollen and Embryo-sacs (n)
Gametes (n)
Fertilised Oosphere (2n) and
F_1 Generation (2n)
(Meiosis)
Pollen and Embryo-sacs (n)
Gametes (n)
Fertilised oospheres (2n) possible combinations and in F_2 generation
TT
tt
T
t
T
t
Tt
T and t
T and t
TT.Tt.tT.tt.

Fig. 411.

When meiosis occurs in the F_1 generation (Tt) it is important to note that the genes for tallness and dwarfness separate and are found in different daughter nuclei. Therefore the individual pollen-grains and embryo-sacs of the flowers of F_1 are *either* T *or* t; *they cannot be* Tt.

Mendel showed that inheritance takes place in a well defined way and cytological studies have now shown the precise mechanism of the process.

In the case of two-character inheritance AABB × aabb illustrated in Fig. 410, the diploid plants of F_1, AaBb will give pollen and embryo-sacs, and hence male and female gametes, possessing either AB, Ab, aB or ab. In other words, we get independent segregation both of chromosomes (and hence of genes) and of characters in the gametes. Further inter-crossing of plants of this F_1 generation permits of the sixteen possible combinations set out in Fig. 410. Thus, for example, a pollen-grain from an F_1 plant AB may germinate on the stigma of another F_1 plant and fertilise an ovule whose oosphere bears, say, aB, giving an oospore, and hence an F_2 generation ABaB, and so on.

12. Subsequent

Mendel's Laws have now been found to hold good in so many cases formerly regarded as obscure or as inexplicable that many now regard them as principles applicable to inheritance in all cases of sexual reproduction, and believe that in conjunction with environmental modification it is sufficient to explain the various " modes of inheritance."

Mendelian theory, however, has been considerably expanded and modified in recent years. It was originally believed that dominant and recessive characters were both represented by definite factors in the germ-plasm, and many still hold this view. It is sometimes held, however, that there is only one factor involved in each pair of differentiating unit characters, and that the dominant and recessive characters are determined by the *presence* and *absence* respectively of the factor. This would give a complete explanation of why we never find A and *a* in the same germ-cell.

It is now known that in certain cases a character may depend not on a single gene, but on two, three, or more genes. Indeed, it has been maintained that most characters depend on a large number of genes and that dependence on one gene is exceptional. It will be evident, from what has been said, that the investigation or analysis of such cases presents great difficulty and, if many genes are involved, may be wellnigh impossible.

Another phenomenon is that of *linkage*, in which two characters are always associated owing to the fact apparently that the genes on which they depend are in the same chromosome and do not become separated during meiosis.

This linkage of characters is well shown in the tomato, where the genes for tallness and smooth skin (both dominant) are linked. The genes for the corresponding recessive characters, dwarfness and peach (hairy) skin are, of course, also linked. If now we cross a pure tall smooth-skinned plant with a pure dwarf peach-skinned one, the sequence of events is as shown in Fig. 412. Here T = Tall, S = Smooth, t = dwarf and s = peach.

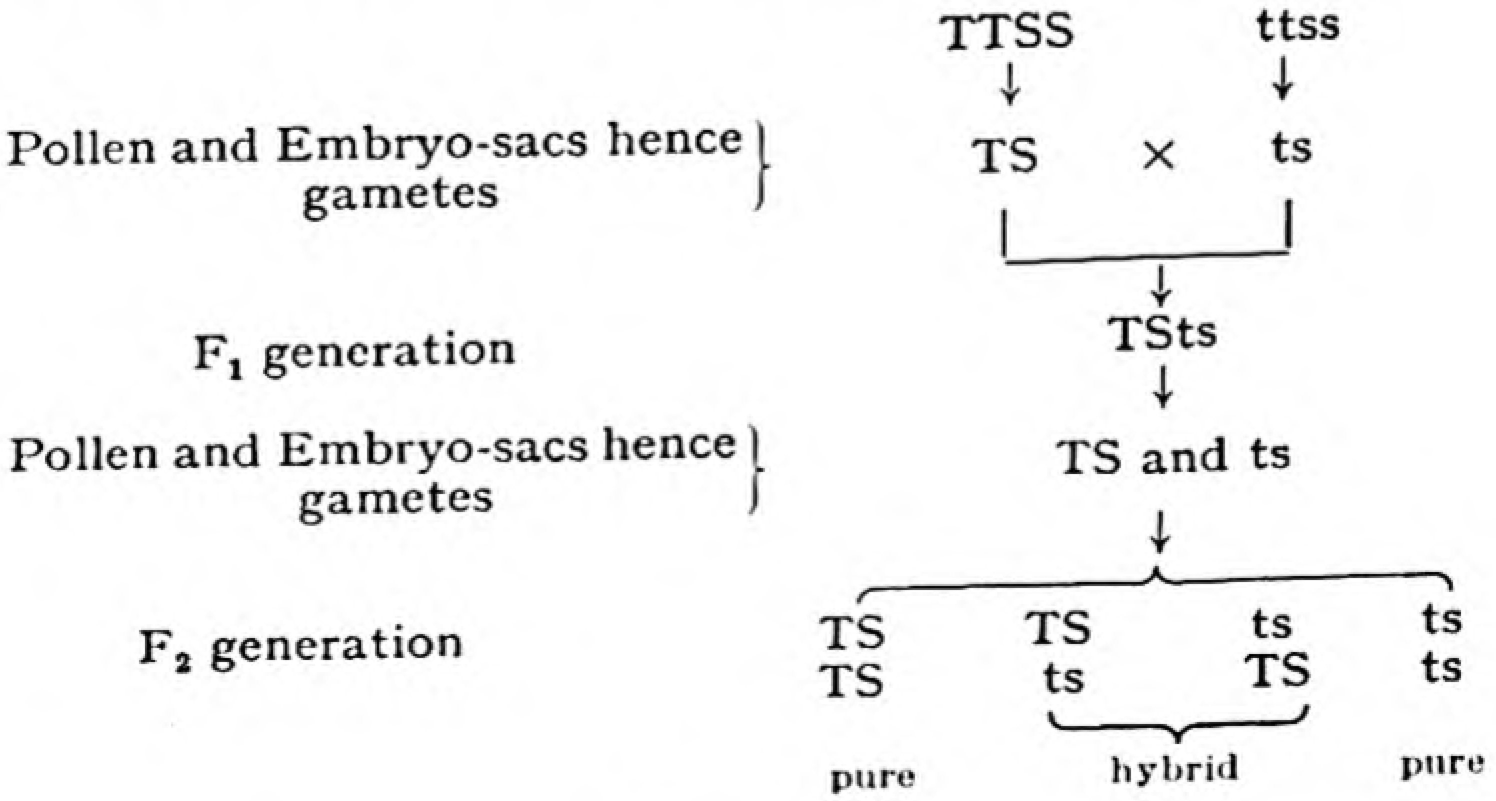

Fig. 412.

In the F_2 generation we have therefore

$\frac{1}{4}$ pure tall smooth;
$\frac{1}{2}$ hybrid tall smooth;
$\frac{1}{4}$ pure dwarf peach.

Because the genes are linked, they are inherited together just like a single gene, and so we have the usual proportion in the F_2 generation of 1 : 2 : 1.

Occasionally deviations from the expected results occur because certain combinations of genes are lethal. We see this, for example, in the case of certain yellow mice. Yellowness is dominant to some other colour, and so we can indicate the yellow hybrids Yy. If these are bred together we might expect to get results as shown below.

Yellow hybrid parents	Yy × Yy		
Possible combinations	YY	$\underbrace{\text{Yy} \quad \text{Yy}}$	yy
Offspring	pure 1 dominant (yellow)	hybrids 2 (yellow)	pure 1 recessive (white)

Fig. 413.

The pure yellow type, however, is not produced because the combination of two dominant yellow genes, YY, is lethal.

Another cause for deviation from the expected results of hybridisation is the phenomenon of " crossing-over " during meiosis (see Chap. IX, § 21). We have already described how this may take place when the spore-mother-cell of the anther divides to give four pollen-grains or microspores, and in the diagram (Fig. 181), two of the latter have chromosomes which contain material, and therefore genes, from *both* male and female parents of the preceding generation. The effect will be seen in the plants of the generation arising from pollination, and fertilisation of ovules, by these pollen-grains.

These and many other cases appear at first sight not to fit in with our conception of inheritance based on the so-called Mendelian principles. Usually, however, the discrepancies are capable of some simple explanation, as in the examples cited.

Many cases of reversion, too, may be explained on Mendelian principles. A recessive character only finds expression if the organism is pure in respect of that character. When indiscriminate breeding takes place, many generations *may* elapse before a pure recessive is produced. When it does happen, we have an organism that in one particular character at least, is unlike both its parents, but resembles one of its more or less remote ancestors. There will be a similar result if a character depends on many complementary genes. Only when all the necessary genes are present does the character appear.

13. The Lamarckian Factor in Evolution

The modern form of Lamarckism, accepted by some biologists (Neo-Lamarckians) as an important subsidiary factor in evolution has already been indicated (§ 5). It is contended that the Lamarckian Factor, if accepted, would provide a much better explanation of certain phenomena and of the evolution of certain classes of characters and structures than either the Darwinian Theory or the Mutation Theory. It is further contended that the study of Palaeontology (including Palaeobotany) shows apparently that evolution has occurred largely, not by the development of anything really new, but by the modification and adaptation of existing structures, and that this is in harmony with the Lamarckian Principle.

14. The Darwinian Theory (1859)

Darwin gave some consideration to the " single variations " (now included in Mutations) which sometimes occur, but considered that they were of little importance in evolution as they occurred so seldom and would be immediately swamped by inter-crossing with the parent forms. He also accepted to some extent Lamarck's Principle as a subsidiary factor. But he relied mainly on the continuous selection of small individual variations. The *Neo-Darwinians* repudiated the Lamarckian factor altogether and laid down Natural Selection as the all-sufficient factor.

Of course, Natural Selection can only act on variations that appear; variation and heredity are the two conditions of evolution. But the Neo-Darwinians believed the action of Natural Selection to be cumulative and that the offspring of selected individuals *tended to vary in the same direction*, so that the varying character was gradually strengthened and intensified. There was thus a tendency to magnify the rôle of Natural Selection and to think of it as a *cause* instead of merely as a factor.

Some Darwinians and Neo-Darwinians would now admit that along with the Natural Selection of small continuous variations, mutation plays an important part in the origin of new varieties and species.

The Selection Theory did not meet with universal acceptance. It was criticised from various points: it was difficult to understand (1) how small individual variations could have selection value; (2) how concomitant selection of small individual variations in different characters could take place and eventually result in structures sharing in a common function; (3) how many structures which have no apparent utility persist and how Natural Selection could have had anything to do with their appearance; (4) Johannsen's demonstration that Natural Selection is ineffective in a pure line, and that there is a limit to its action in a population, together with the probable conclusion that continuous variation is largely of the nature of environmental effect. Selection, therefore, would be operative only in that from a mixed population, one or more pure, or nearly pure, lines might be separated. Once this point is reached, only fluctuating variations, which are not inherited, occur.

15. The Mutation Theory (see § 6)

This theory got rid of the difficulties mentioned above. Mendelism greatly helped by demonstrating that there was no danger of a new character, if it were a Mendelian character, being lost by intercrossing with the parent form. According to the Mutation Theory Natural Selection is still a factor, but its action is restricted to the elimination of forms due to mutation, which are not fitted for their environment. As de Vries expresses it, "Natural Selection may explain the survival of the fittest, but it cannot explain the arrival of the fittest."

We have seen (§ 10) that new forms or species may arise by new combinations of characters in crossing or hybridisation. By some these new combinations, depending on new grouping of factors in the germ-cells, are included under the term mutations. Usually, however, by mutations are meant really new forms appearing more or less suddenly. In the combinations referred to there is nothing really new.

It will be evident that if we accept the Mutation Theory it is more than ever necessary to determine the origin and causes of variation or mutation, for it is on mutation that the chief stress is laid. Some recent workers believe that they have evidence of the origin of *new factors*, both dominant and recessive, by definite changes, probably chemical in nature, occurring in certain parts of the chromosomes, factors either entirely new or due to modification of existing factors. The changes may apparently be induced by internal or external stimuli. There is evidence to show that mutations may be induced by external influences (e.g. exposure to X-rays), but many mutations apparently arise spontaneously. Gene mutations occur, and not infrequently a chromosome may fragment, and the detached piece of chromosome either join up with another chromosome, remain separate, or join with another fragment. When a cell in which this has occurred undergoes meiosis, some of the resulting reproductive cells will carry extra genes and some will be short of their " normal " gene complement. This gives rise to the possibility of an almost infinite number of new combinations of characters, not simply unlike their parents, but unlike any of their ancestors, and, in fact, quite new.

Sometimes, too, the complement of chromosomes, and hence of genes, in a cell undergoes a doubling. If this results in the production of diploid pollen and embryo-sacs, then we may get a diploid male gamete fusing with a haploid female gamete (to give a triploid fertilised oosphere (*i.e.* one with $3n$ chromosomes), or two diploid gametes may fuse to give a tetraploid fertilised oosphere. In this way plants with several complements of chromosomes may arise. These polyploids, as they are called, are really new species. This is doubtless the way in which many species have arisen. As the new forms appear suddenly they are classed as mutations. When mutations, however caused, do occur, natural selection will become operative. Many of the mutations produced will not survive. Others will not only survive and constitute new species, but, because of enhanced vigour, or increased tolerance of unfavourable conditions, may soon come to cover large tracts of land. The rice-grass (*Spartina Townsendii*), which is a polyploid believed to have arisen by the natural hybridisation of two other species of *Spartina*, is an example of this. It is more vigorous than either parent, and has established itself in areas where neither parent can grow successfully.

APPENDIX

I. GENERAL ADVICE TO THE STUDENT

1. Reading.—The necessity of careful reading cannot be too strongly insisted on. The student should be on his guard against the tendency to rapid reading. Before passing from one part of the subject to another he should make sure, as far as he can, that he has understood what he has read. A habit of skipping difficulties is easily acquired and not easily overcome. There may be occasions when even the most diligent application will fail to clear up difficult points, and where persistence in wrestling with them only results in a waste of time. In such cases the student should for future reference make a note of the points he has failed to master. It may be that a wider knowledge of the subject will make them clear.

Special reference may here be made to the first two chapters of the present textbook. These chapters deal with general facts and principles, and it is not expected that, at the first reading, the student will acquire a perfect knowledge of their contents. They may be used for purposes of reference, and should be carefully revised at a later stage.

However careful the reading, it is of little use unless accompanied by practical work. This will be specially dealt with in Sections II and III of the Appendix.

2. Diagrams and Drawings.—In connexion with the practical work the student should, besides keeping a record of his experiments and observations, make clear, outline pencil-drawings of the specimens examined or the sections cut. The making of drawings gives precision to the work besides helping the memory; it impresses on the student's mind not only the more important points, but also many details which might otherwise be overlooked. It is advisable that the drawings should be made, wherever possible, to some definite scale.

Shading should generally be avoided, and drawings may frequently be semi-diagrammatic. Increased clarity in the drawings is obtained if a moderately hard pencil and smooth paper are used. The rough paper in most " drawing books " is unsuitable.

3. Test Questions.—Those who are responsible for drawing up courses of study carefully select types, so that these may be used not only for factual knowledge but also for illustrating basic principles. The student who understands foundation principles can apply his knowledge to new problems. It is a mistake to try to learn facts, so as to be able to reproduce them without even attempting to understand their significance. Examination questions are often framed so as to test the student's understanding of principles, and the ideal examinee is the one who is able to expound these principles in his own words, using as illustrative examples the types with which he is familiar, and making clear, labelled drawings wherever it is possible in order to further clarify his statement. Sometimes questions require the comparison or contrast of certain organs or structures. The tabular method of answering such questions is in general undesirable.

4. Botanical Terms: Greek and Latin Roots.—Many botanical terms have departed so far from their original meanings, as implied in their etymology, that the student must get to know them in the same way as he would get to know the words in learning a new language. Frequently, however, a knowledge of the derivation of botanical terms is really helpful; for this reason we give here a table of Greek and Latin roots which may be of service to the student:—

GREEK

a-, *without* (apetalous); **acro-**, *summit* (acropetal); **actino-**, *rayed* (actinomorphic); **adelphos**, *brother* (monadelphous); **amphi-**, *both* (amphibious); **ana-**, *up* (anabolism); **andr-**, *of man* or *male* (androecium); **anemos**, *wind* (anemophily); **angios**, *a vessel* (angiosperm); **anti-**, *opposite* (antipetalous); **apo-**, *away from* (apocarpous); **bio-**, *life* (biology); **blema**, *covering* (epiblema); **bolos**, *a throwing*; **carp**, *fruit* (epicarp); **cata**, *down* (catabolism); **chlamys**, *a cloak* (archichlamydeae); **chloro-**, *green* (chlorophyll); **chromo**, *colour* (chromoplast); **cleisto-**, *closed* (cleistogamous); **cyto-**, *cell* (cytoplasm); **derma**, *skin* (epidermis); **di-**, *twice* (dicotyledon); **dich-**, *apart* (dichotomous); **dynamis**, *strength* (tetradynamous); **endo-**, *within* (endocarp); **epi-**, *on* (epidermis); **ergon-**, *work* (energy); **gamos**, *marriage* (polygamy); **ge**, *earth* (geotropism); **-gen**, *producing* (endogenous, oxygen); **gyn-**, *of woman* or *female* (gynaeceum); **helios**, *sun* (heliotropism); **heteros**, *different* (heterogamous); **histos**, *web, tissue* (histology); **homos**, *same* (homology); **hypo-**, *under* (hypodermis); **logos**, *science* (physiology); **mega-**, *large* (megaspore); **meros**, *part* (mericarp); **meso-**, *middle* (mesocarp); **micro-**, *little* (microspore); **mono-**, *single* (monadelphous); **morphe**, *form* (morphology); **-oecium (oikos)**, *house* (androecium); **-oid**, *like* (bacteroid); **oon**, *an egg* ; **orthos**, *straight* (orthostichies); **peri-**, *around* (pericycle); **-phile**, *loving* (hydrophilous); **phobe**, *hating* (photophobic); **-phore**, *carrying* (carpophore); **phyll**, *leaf* (mesophyll); **phyte**, *plant* (spermatophyta); **plasma**, *anything formed* (protoplasm); **pod**, *foot* (monopodial); **poly**, *many* (polypetalous); **protos**, *first* (protoplasm); **pseudo**, *false* (pseudocarp); **rhiza**, *a root* (rhizoid); **sapros**, *putrid* (saprophyte); **schizo**, *split* (schizocarp); **scleros**, *hard* (sclerenchyma); **sperma**, *seed* (endosperm); **stichos**, *a row* (orthostichies); **syn-**, *together with* (syncarpous); **tetra**, *four* (tetradynamous); **thec**, *a case* (theca); **tropos**, *direction* (heliotropism); **xero-**, *dry* (xerophilous); **zygon**, *a yoke* (zygomorphic); **xylon**, *wood* (xylem).

LATIN

ad, *to* (adhesion); **albus,** *white* (alburnum); **amplexus,** *embraced* (amplexicaul); **arena,** *sand* (arenaceous); **argilla,** *clay* (argillaceous); **auriculus,** *little ear* (auriculate); **axilla,** *armpit* (axil, axillary); **bacillum,** *little staff* (bacillus); **bi-,** *twice* (bifid, bipinnate); **bulbus,** *onion* (bulb); **caducus,** *fallen* (caducous); **capillus,** *hair* (capillary); **capitulum,** *little head*; **capsula,** *little box* (capsule); **carcer,** *prison* (carcerulus); **carn-,** *flesh* (carnivorous); **caruncula,** *small piece of flesh* (caruncle); **caulis,** *stem* (caulicle); **com-** (**cum**), *with* (compound, collateral); **corona,** *crown*; **corolla,** *little crown*; **corymbus,** *bunch of flowers* (corymb); **cutis,** *skin* (cuticle); **decurro,** *to run down* (decurrent); **decusso,** *to divide crosswise* (decussate); **dehisco,** *to open* (dehiscent); **duramen,** *hardness*; **equito,** *to ride on horseback* (equitant); **ex,** *without* (exalbuminous); **-fid,** *cleft* (pinnatifid); **fistula,** *pipe* (fistula); **flaccidus,** *withered* (flaccid); **flos,** *flower* (floral); **folia,** *leaf* (foliage); **folliculus,** *little bag* (follicle); **fugo,** *to flee* (fugaceous); **glaber,** *smooth* (glabrous); **glaucus,** *bluish grey* (glaucous); **hasta,** *spear* (hastate); **haustus,** *drawing up water* (haustorium); **hispidus,** *bristly* (hispid); **humus,** *soil* (humus); **imbrex, -icis,** *a roof tile* (imbricate); **impar,** *unequal* (imparipinnate); **inter,** *between* (intercellular); **involucrum,** *cover* (involucre); **labium,** *lip* (labiate); **lignum,** *wood* (lignified); **ligula,** *strap* (ligulate); **loculus,** *little place* (trilocular); **nectar,** *honey*; **nodus,** *knot* (node); **nuto,** *to nod* (nutation); **nux,** *nut* (nucellus); **ovum,** *egg* (ovule); **papilio,** *butterfly* (papilionaceous); **par,** *equal* (paripinnate); **paries,** *wall* (parietal); **pelta,** *shield* (peltate); **persona,** *mask* (personate); **peto,** *to seek* (acropetal); **pinna,** *wing* (pinnate); **pluma,** *feather* (plumule); **pulvinus,** *cushion*; **pyxis,** *box* (pyxidium); **racemus,** *bunch of grapes* (raceme); **radix,** *root* (radicle); **renes,** *kidney* (reniform); **rota,** *wheel* (rotate); **sagitta,** *arrow* (sagittate); **sectus,** *cut* (pinnatisect); **serra,** *saw* (serrate); **siliqua,** *pod* or *shell*; **subula,** *awl* (subulate); **umbella,** *parasol* (umbel); **urceolus,** *little pitcher* (urceolate); **vas,** *vessel* (vascular); **versatilis,** *revolving* (versatile); **verticillus,** *whirl of a spindle* (verticillate).

5. Supplementary Reading.—It is of advantage to read other textbooks, in order to benefit from the point of view of the various authors and to develop a critical faculty in reading. Some students may be desirous of further extending their botanical studies, and of specialising in a particular branch of the subject. The following books are recommended:—

(*a*) **General Textbooks.**—Bower, *The Living Plant*; Strasburger, *Textbook of Botany*.

(*b*) **Special Studies.**—Arber, *Monocotyledons*; Bower, *Ferns*; Campbell, *Mosses and Ferns*; Chamberlain, *Structure and Evolution of the Gymnosperms*; Eames and MacDaniels, *Introduction to Plant Anatomy*; Fritsch, *Structure, and Reproduction of the Algae*; Gwynne-Vaughan, *Fungi*; Gwynne-Vaughan and Barnes, *The Fungi*; Haas and Hill, *Chemistry of Plant Products*; Hutchinson, *Dicotyledons, Monocotyledons*; Rendle, *Classification of the Flowering Plants: I. Dicotyledons, II. Monocotyledons and Gymnosperms*; Russell, *Soil Conditions and Plant Growth*; Scott, *Studies in Fossil Botany*; Steele, *Introduction to Plant Biochemistry*; Stiles, *Introduction to the Principles of Plant Physiology*; Tansley and Chip, *Aims and Methods in the Study of Vegetation*; Walton, *Fossil Plants*.

(*c*) **For General Reading or Reference.**—Bower, *Size and Form in Plants*; Darwin, *Origin of Species*; *Climbing Plants*; *Insectivorous Plants*; Haberlandt, *Physiological Plant Anatomy*; Large, *The Advance of the Fungi*; Schimper, *Plant Geography*; Scott, *Evolution of Plants*; Skene, *Biology of Flowering Plants*; Willis, *Dictionary of the Flowering Plants and Ferns*.

(*d*) **Floras.**—(i) General. *Icones plantarum Indicae orientalis*; Burmann, *Flora indica*; Hooker, *Flora of British India*; Wright, *Illustrations of Indian Botany*. (ii) Regional. Cooke, *Flora of the Presidency of Bombay*; Roxburgh, *Coromandel Plants*; Don, *Prodromus florae Nepalensis*; Duthie, *Flora of the Upper Gangetic Plain*; Gamble, *Flora of the Presidency of Madras*; Trimen, *Handbook of the Flora of Ceylon*.

II. Notes on Practical Work

6. Examination of Plants.—The student should devote a considerable amount of time to the study of complete plants, and the examination of special parts. He should carefully notice the different kinds of roots and stems, and accustom himself to the use of the various terms explained in the text. Bulbs, tubers, corms, rhizomes, suckers, etc., should be studied, and their special features recognised. The morphological nature of spines or thorns, tendrils, and other specialised structures, wherever specimens present themselves, should be clearly made out. The form, arrangement, and venation of leaves; branching; the position of buds, stipules, bracts, etc.; the forms, etc., of corolla, androecium, and gynaeceum; the seed and fruit, etc.;—all these should be subjected to careful examination.

In the examination of minute or crowded parts, as for example, in the case of many flowers, it will be found not only convenient, but necessary, to use a **hand-lens.** A very convenient folding form, with three glasses, can be obtained from any dealer. For finer work, a simple dissecting stage, with lenses, is needed.

7. Physiology.—A practical knowledge of the nutrition and growth of plants is essential. The student, therefore, should carry out as many simple experiments as he can.

8. Microscopic Work.—We cannot give here full detailed directions about section-cutting and the making of preparations for microscopic examination. The student is strongly advised to attend classes at an institution where practical instruction can be obtained.

9. Apparatus.—The following equipment is necessary:—

(*a*) A good microscope with objectives $\frac{2}{3}$ and $\frac{1}{6}$ in. focal distance, and eye-pieces II and IV.

(*b*) Two good razors, slightly hollow-ground, a razor-strop.

(*c*) Glass slides, 3 in. × 1 in.; cover-glasses, $\frac{7}{8}$ in. diam. or sq.

(*d*) Small forceps, dissecting needles, and scalpels.

(*e*) A few deep watch-glasses; small brushes; a clean piece of soft linen.

(*f*) Pickle jars, methylated spirit, formalin (see § 13).

(*g*) Small dropping bottles (or with dipping rods) containing iodine solution, aniline sulphate (or chloride), Schulze's solution, glycerine, etc.

(*h*) A spirit lamp, test-tubes.

10. Cutting and Mounting Sections.—At first the student should content himself with sections stained with iodine or other suitable stain (§ 11) and mounted in dilute glycerine. Only if time permits, and after considerable experience in this method should he attempt more elaborate methods of staining and mounting.

In taking a section, the tissue to be cut should be held between the thumb and fingers of the left hand; the razor in the right hand. The tips of the four right fingers should rest on the back of the razor, and the thumb in front, just behind the cutting edge. The cutting edge is therefore directed inwards, towards the operator. The arms should be brought close up to the body. Tissue and razor should both be wet with alcohol (or water if fresh material is being used). The blade of the razor may rest gently on the forefinger of the left hand with the edge against the tissue. Then the razor should be drawn through the tissue with a sliding movement. *With practice*, extremely thin sections may be cut.

The sections should be removed from the razor by means of a brush, and placed in a watch-glass containing alcohol or water. Several may then be transferred to a slide and examined in water under the low power, so that the best may be selected. By means of a linen cloth or blotting paper the excess of water may be removed, and iodine or other reagent added according to the special points which the student wishes to determine. The reagent should then be washed off with water, the excess of water removed, a drop of dilute glycerine added, and finally the cover-glass put on.

A useful method of employing reagents is known as the method of irrigation. The section is mounted in water on a slide under a cover-glass (preferably square) and focused under the low power of the microscope. Two or three drops of the reagent are applied to one side of the cover-glass (taking care not to wet the surface of the cover-glass) and a piece of blotting paper is applied to the opposite side. The reagent gradually replaces the water and its action on the preparation can be observed as it does so.

The section should always be mounted in the centre of the slide. The cover-glass should be rested on its edge and let down gradually by means of a needle. The section *must not be allowed to get dry* during the process, or air-bubbles will make their appearance. If these do appear, soaking the section for some time in alcohol will help to remove them. The cover-glass must be perfectly clean, and the upper surface dry.

Neatness and cleanliness are of great importance in practical work. At first the student will find that his sections are rather thick, and often obliquely cut. These are difficulties which can be got over only by care and practice. He should not attempt to draw a bad section.

Very slender or delicate tissues should be cut by embedding in pith or carrot. More elaborate methods may be passed over in early stages of practical work. If carrot is used, a piece 1 in. × ½ in. × ¼ in. will be found convenient.

11. Useful Reagents, etc.—The following particulars, although very brief, will be helpful to the student:—

Acetic Acid, 33 per cent.; calcium oxalate is insoluble, calcium carbonate dissolves with effervescence.
Alcohol, Absolute, for dehydrating preparations before permanently mounting.
Alcohol, commercial, in various dilutions, has many uses.
Alkanna, Tincture of, for staining fixed oils.
Aniline Chloride (or Sulphate) stains lignified walls yellow.
Canada Balsam, for making permanent mounts.
Chloral Hydrate solution, 5 gm. chloral hydrate to 2 c.c. water, a clearing agent which dissolves most cell contents (not calcium oxalate), and swells out dried, collapsed tissues.
Chlorzinciodine (Schulze's Solution) differentiates cellulose (blue) lignin and suberin (yellow-brown) and starch (swells, stains blue). Stains protoplasm brown. Deteriorates with age.
Corallin soda stains the callus plates of sieve-tubes (use freshly made).
Cuoxam (Schweizer's Reagent, Ammoniacal Copper Oxide) dissolves cellulose, but should be freshly made.
Eau de Javelle, a clearing agent.
Fehling's Solution for detecting reducing sugars.
Ferric Chloride, 1 per cent. solution, for tannin.
Glycerin, pure or dilute, a mounting medium.
Hydrochloric Acid, dissolves calcium oxalate: see also phloroglucin.
Iodine water, or Iodine in Potassium Iodide, stains starch (blue-black), aleurone grains (yellow), suberised and lignified walls (yellow), cellulose walls (yellow turning blue on irrigating with conc. sulphuric acid).
Lactophenol, a mounting medium; can be used with various reagents in solution, e.g. iodine for starch, cotton blue for fungal hyphae, etc.

Macerating Fluid, fuming Nitric Acid and Potassium Chlorate, destroys the middle lamellae of woody tissues and separates the elements.

Methylene Blue, weak alcoholic solution or with glycerin, stains mucilage.

Millon's Reagent, stains protein brick-red on warming.

a-Naphthol, alcoholic solution, in conjunction with sulphuric acid gives an intense violet colour with inulin.

Phloroglucin, alcoholic solution, with strong hydrochloric acid stains lignified cell-walls red.

Picric acid, saturated aqueous solution, stains aleurone grains yellow.

Potash, 5 per cent. solution; a clearing agent, dissolves cell contents; also a macerating agent for parenchyma and phloem.

Ruthenium red, solution in lead acetate, stains mucilage a brilliant pink colour (use freshly made).

Sudan III, alcoholic solution or with glycerin, stains fixed and volatile oils, and suberised walls.

Sulphuric Acid, concentrated, destroys cellulose and lignified cell-walls, but not suberised walls, nor the middle lamella of lignified cell-walls. See also iodine.

12. Drawings of Microscopic Preparations.—Preparations must be examined under both low and high magnifications. Generally, viewing the section or other preparation, with the low-power objective, a diagram should be drawn to show the general shape of the section and the distribution of the different tissues in it. It is unwise to attempt to show in such a diagram any drawings of individual cells. Using the high-power objective, detailed drawings should be made. Sometimes a series of drawings, to illustrate the structure of all the tissues is called for. At other times a complete segment of a section may be drawn in detail. It is generally unnecessary and wasteful of time to draw large numbers of cells. Two or three cells drawn accurately are of greater value, and give a truer picture of the structure of a particular tissue than large numbers of cells drawn carelessly and inaccurately and to such a small scale that structural details cannot be shown. It is generally an error to attempt to make drawings illustrating the anatomical structure of stems, leaves, and other organs like those used to illustrate a textbook. Textbook drawings are usually made on a large scale and then reduced in reproduction. Only in this way can a wealth of detail be shown in a drawing of small compass. To attempt to make detailed drawings directly on a small scale is to court disaster. It cannot be over emphasised that to show detail, large-scale drawings are essential.

13. Material.—Fresh material may and sometimes must be used. In many cases, however, it is better and more convenient to use " pickled " material. The pickling fluid used for ordinary work is ordinary methylated spirit. Stems, roots, leaves, etc., preserved in this way in glass jars are always ready for use. Delicate plants or parts of plants (flowers, etc.) may be preserved in a four to six per cent. solution of formalin (formaldehyde); formalin as sold is a forty per cent. solution. This method has the advantage of preserving colours. Types such as *Vaucheria*, *Spirogyra*, *Oedogonium*, *Eurotium*, Yeast, are best examined in the living state.

The student is advised to obtain material himself, as far as possible. With Angiosperms, Gymnosperms, and fern there is usually no difficulty. *Pellia*, *Funaria*, *Oedogonium*, *Spirogyra*, *Ulothrix*, and *Vaucheria* may be collected. Fern prothalli can usually be obtained in abundance on the damp walls or on the soil or surfaces of flower-pots in fern-houses. Directions for obtaining *Pythium*, *Eurotium*, etc., are given in our descriptions of these types. Yeast may be obtained from a baker, or brewer.

14. Practical Work on Angiosperms.—As the student may be in some doubt as to the practical work which should be undertaken in connexion with the Angiosperm, the following list may be of service.

Stems.—Transverse and longitudinal sections of young herbaceous dicotyledonous stems (e.g. *Helianthus*, *Solanum*, *Cucurbita*) and of woody stems. Also of such Monocotyledons as *Asparagus*, maize and *Dracaena*. Specialised types such as aquatic plants, succulents (*Opuntia*, *Kleinia*, etc.) should be examined. The beginnings of secondary thickening may be studied in *Helianthus* or *Ricinus*.

Buds.—Longitudinal sections of Brussels sprouts, *Aesculus*, etc. Try to make out the primary meristematic region.

Roots.—Transverse sections of such roots as maize, leek, broad bean, *Ricinus*, *Helianthus*, etc. The apical meristem can be studied in median longitudinal sections of the radicles of maize, almond, sunflower and *Ricinus*. Root-hairs may be obtained by germinating cress or mustard seed in saturated air.

Leaf.—Sections of petiole and lamina of both isobilateral and dorsiventral types. Strips of epidermis from both surfaces should be examined. Specialised leaves such as those of succulent plants (e.g. *Aloe* and *Kleinia*), of insectivorous plants (*Drosera*), etc., should be studied. Portions of thin leaves, cleared by boiling with chloral hydrate, may be examined for epidermal hairs, stomata, venation, etc.

Flower.—Sections of ovaries and anthers. The structure of the ovary, the placentation, the form and structure of the ovules, should be recognised. The form and structure of the ovule can usually be readily made out in sections of ovaries, or, if the ovules are small, by examining entire after treatment with dilute potash solution.

Seeds.—In examining a seed the student should determine by means of sections and staining if the seed is dicotyledonous or monocotyledonous, endospermous or non-endospermous and the nature of the food-material.

Contents of Cells and Structure of Cell-Walls.—These should be carefully studied in connexion with the above. To see such bodies as cystoliths and raphides the student should try to obtain the material mentioned in the textbook.

III. DESCRIPTIVE BOTANY

15. Description of Plants.—Accurate description of plants or parts of plants, especially if not accompanied by drawings or photographs, is important for those who are concerned with their uses. The earliest botanical works consisted of descriptions and figures of plants used in medicine, and as the interest in Botany widened to include all kinds of plants, so greater accuracy of description was required in order to enable botanists to identify them. This aspect of Botany is now largely the concern of systematists, and specialists in such subjects as pharmacognosy (materia medica), plant-breeding, economic products, etc.

The following scheme indicates the order in which such descriptions should proceed. It is intended only as a guide, but will rarely be needed by the student.

Root: tap or adventitious? branched or unbranched? the special form—tuberous, fleshy, fibrous, etc.? annual, biennial, or perennial?

Stem: kind of stem—*i.e.* is it erect, prostrate, or climbing? a rhizome, corm, or bulb, etc.? herbaceous or woody? green or other colour? cylindrical, angular, or compressed? hairy or glabrous? branched or unbranched (the branching may be described)? If herbaceous, is it solid, hollow (fistular), or jointed? If woody, give the surface characters of the bark. If climbing, how does it climb? Does it bear cladodes, tubers, spines, etc.?

Leaf: deciduous or evergreen? radical, cauline, or ramal? alternate, opposite (superposed or decussate), or verticillate? petiolate or sessile? stipulate or exstipulate (the stipules may be described)? sheathing, connate, perfoliate, ligulate, etc.? simple or compound?

If simple, outline of lamina (*i.e.* linear, oval, etc., or pinnatifid, palmatifid, etc.—if incised, the outline of the lobes, partitions, or segments may be indicated)? venation? margin? apex? base? surface (glaucous, hairy, etc.)?

If compound, pinnate or palmate? paripinnate or imparipinnate? number and arrangement of leaflets? *Leaflets*—sessile or stalked? outline? venation? margin? apex? surface?

Inflorescence: definite, indefinite, or mixed? kind of inflorescence? characters of axis (elongated, conical, flattened, concave, solid, hollow, etc.)?

Flowers: sessile or pedicellate? bracteate or ebracteate (if bracteate, the bracts may be described)? complete or incomplete? hermaphrodite or unisexual? actinomorphic, zygomorphic or asymmetrical? cyclic, hemicyclic or spiral? heterostylic? any other general character?

If there are two kinds of flowers, after giving common characters as above, describe separately.

Calyx: poly- or gamo-sepalous? green or petaloid? if polysepalous, the number, outline, and apex of the sepals? if gamosepalous, the special form or nature of the incision? inferior or superior? aestivation?

Corolla: regular or irregular? if irregular, zygomorphic or asymmetrical? poly- or gamo-petalous? if polypetalous, number and outline of petals, or any special terms? if gamopetalous, special form or incision? corona or other special features? hypogynous, perigynous, or epigynous? aestivation?

Perianth: described similarly, except that the terms poly- or gamo-phyllous must be used.

Androecium: number of stamens? or indefinite? polyandrous, syngenesious, or adelphous? epipetalous, epiphyllous, hypo-, peri- or epi-gynous? special characters? filament? fixation of anther? dehiscence?

Gynaeceum: mono- or poly-carpellary? if the latter, apo- or syn-carpous? *Ovary*—unilocular or multilocular? superior or inferior? *Ovules*—number? or indefinite? form? *Placentation*? *Style*? *Stigma*?

Seed: endospermous or non-endospermous? perisperm present or absent? embryo, position, shape, size? cotyledons, straight, folded, etc.? radicle, incumbent, accumbent, etc.?

Fruit: kind of fruit?

Nectaries may be described in connexion with corolla, stamens, or pistil, as seems convenient.

16. Examples.—The following descriptions of two plants will serve as examples:—

(1) SINAPIS ALBA, L. [= Brassica alba (L.) Boiss], White Mustard

Root: a fibrous branched tap-root; annual.

Stem: erect; branched; angular; herbaceous; hairy; annual.

Leaves: herbaceous; cauline; petiolate; exstipulate; simple; lyrate; unicostate; reticulate; obtuse; pinnatipartite; hairy.

Inflorescence: indefinite—terminal and lateral, more or less corymbose racemes.

Flowers: pedicellate; ebracteate; isobilateral; hermaphrodite.

Calyx: polysepalous; four lanceolate spreading sepals in two series, the two inner (lateral) sepals slightly pouched (saccate); inferior.

Corolla: regular, polypetalous, cruciform, consisting of four unguiculate, yellow petals; *limb* obovate; hypogynous; imbricate.

Androecium: six stamens in two series; tetradynamous; two short lateral stamens; two pairs, anterior and posterior, of long stamens; hypogynous; *anthers* innate, introrse, with longitudinal dehiscence. *Nectaries*, having the form of green, rounded discs, are present at the base of the lateral stamens.

Gynaeceum: bicarpellary, syncarpous; *ovary* bilocular, owing to a false septum developed between the placentas, superior; *ovules* ∞, campylotropous, on two parietal placentas; *style* short; *stigma* two-lobed.

Seed: non-endospermous, in a single row, globose in shape, cotyledons conduplicate, $<<$o.

Fruit: an elongated, linear, beaked and terete or angled siliqua, hispid; fruit-stalks fairly long, stand out at right angles to the peduncle.

(2) FRAGARIA NILGERRENSIS, Schlecht, Wild Strawberry

Roots: adventitious, fibrous, and stout, yellowish.

Stem: woody, perennial, underground, covered with brown scales, and throwing out long slender runners which root at the nodes.

Leaves: radical, with long hairy petioles and membranous, lanceolate, stipules adnate to the petiole; compound, ternate; *leaflets* nearly sessile, roundish oblong, with unicostate reticulate venation and coarsely dentate margin.

Inflorescence: panicled, more or less corymbose, cymes borne on erect slender scapes. Peduncles densely golden-villous, 2·5-4·0 cm. long.

Flowers: pedicellate, with leafy bracts; actinomorphic; complete; hermaphrodite; protogynous.

Calyx: gamosepalous, with five membranous, triangular, acuminate segments; green, persistent, inferior; an epicalyx is present consisting of five deeply bifid segments with lanceolate lobes alternating with those of the calyx proper.

Corolla: regular polypetalous, rosaceous, consisting of five white roundish petals inserted perigynously.

Androecium: polyandrous; *stamens* ∞, persistent, perigynous; *filaments* short and stiff; *anthers* oval to more or less cordate, dehiscing laterally.

Gynaeceum: polycarpellary, apocarpous; *carpels* indefinite, and borne on a protuberance of the receptacle, with filiform styles and simple stigmas; *ovules* solitary, ascending.

Seed: minute, non-endospermous, dicotyledonous.

Fruit: a pseudocarp consisting of an etaerio of achenes borne on a succulent receptacle. Ripe receptacle white tinged with pink.

TEST QUESTIONS

1. Give an illustrated account of the structure of the seed and the mode of germination of pea, wheat (or maize), cress, and lupin.

2. Give an account of the functions, and the behaviour during germination, of the cotyledons in various seeds whose germination you have watched.

3. What food reserves are commonly found in seeds? By what tests would you recognise them? How do they become available to the young plant at the time of germination?

4. Examine and draw the twigs of *Aesculus*, jujube (*Zizyphus*), pipul (*Ficus religiosa*) and kapok (*Eriodendron*) when the resting buds are beginning to unfold.

5. Describe the various morphological structures in plants which may constitute aids to climbing.

6. Describe, with drawings, the internal structure of a named bulb and a named corm.

7. Describe various methods in which plants may reproduce themselves vegetatively.

8. How would you distinguish between (*a*) a simple leaf and a cladode, (*b*) a compound leaf and a short branch?

9. What are meristematic tissues? Give an account of the meristematic tissues found in dicotyledonous stems.

10. How are new cells formed at the apex of a stem or root? Give an account of the phenomena observed in connexion with cell-formation there.

11. Describe the structure and development of an open, collateral vascular bundle, and indicate the functions of the various parts.

12. Describe the structure, as seen in transverse section, of a twig of any named dicotyledonous tree.

13. What elements are formed as a result of cambial activity? Trace the changes that take place between the division of a cambium cell and the differentiation of a vessel.

14. How is cork formed and where is it found in a woody shoot?

15. Give an account of the process of Mitosis.

16. What structural differences would you expect to find in the stem of a water-plant (e.g. *Myriophyllum* or *Trapa*) as compared with that of an ordinary herbaceous land-plant?

17. What are the functions of the foliage leaves in an ordinary land-plant? Describe the structure of any named dicotyledonous leaf.

18. Describe the structural characters of the epidermis of the stem of the sunflower, or of any other herbaceous Dicotyledon you may select.

19. What is sclerenchyma? Describe its structural characters, and give some account of its distribution and functions in the stems and leaves of flowering plants.

20. Mention the more important structural differences between roots and shoots. Show how these differences can be related to function-differences.

21. Describe the processes of tissue-differentiation that take place at a shoot-tip.

22. Give a short account of the structure, development, and functions of cork in a named dicotyledonous stem.

23. What is understood by secondary growth? What is its significance? Describe the process as seen in the stem of any named Dicotyledon.

24. Describe, in the case of a dicotyledonous tree, the mode of origin and growth of a lateral branch. Name in order, from the centre outwards, the tissues that you would expect to find in a transverse section taken at the base of the branch at the end of the third year.

25. What are the more important anatomical differences in stem, leaf, and root which would enable you to distinguish a monocotyledonous from a dicotyledonous plant?

26. Give a short account of the phenomena observed in connexion with the fall of leaves in trees.

27. How does the nutrition of an animal differ from that of a green plant?

28. Give an account of the process of water-absorption by a root-hair.

29. What substances (other than water) are absorbed by the roots of a land-plant?

30. Describe experiments which demonstrate that the green land-plant obtains its carbon from the air.

31. Enumerate the chemical elements that analysis reveals to be present in a green plant, and indicate their functions in the plant.

32. What is root-pressure? How would you demonstrate and measure it?

33. Give an account of the function of chlorophyll. Under what conditions is it developed?

34. How would you prove that many green plants synthesise starch when exposed to light?

35. What is a carbohydrate? Mention the chief carbohydrates, stating how they are distinguished from each other. How are oils and fats distinguished from carbohydrates?

36. Under what conditions can a green plant form starch? Give an account of the experimental evidence on which your answer is based.

37. Give a general account of the structure, origin, occurrence, and functions of plastids.

38. Explain how you would proceed to make a water-culture. Indicate the effect on the plant of the omission from the culture solution of iron, calcium, potassium, and nitrogen respectively.

39. Of what substances do the crystals found in plant-cells usually consist? Under what circumstances are these crystals formed?

40. Describe experiments you have made on transpiration, and explain how the rate of transpiration is affected by external conditions.

41. Bubbles ot gas arise when a green water-plant in a bowl of ordinary tap-water is placed in sunlight. What is this gas and how is it produced? Give as full an explanation as you can of the effect of (*a*) replacing the tap-water by previously boiled water, (*b*) replacing it by 0·5 per cent. sodium bicarbonate solution.

42. In what tissue does the water ascend in a stem in its passage from root to leaf? How would you endeavour to prove by experiment the truth of your statement?

43. What is growth? What are the conditions necessary for growth? Give an account of the properties exhibited by growing points.

44. Name the necessary conditions of germination, and describe experiments, which you have seen or performed, which illustrate your statements.

45. What is respiration? How would you demonstrate that it takes place in plants? How is the process affected (*a*) by heat, (*b*) by light?

46. Describe exactly how you would obtain the dry weight of a seedling. What difference would you expect to find between the dry weight of (*a*) a seed, (*b*) a seedling of the same plant grown in the dark for some time, (*c*) a similar seedling grown under normal conditions for the same time?

47. Describe accurately an experiment which you have seen in which the rate of growth of shoots or roots was measured. Which part of the root grows most rapidly in length and which part absorbs most water?

48. The trunk of a dicotyledonous tree, when in full leaf, is sawn all round so deeply as to cut through the sap-wood. State and explain the effect of this operation.

49. Describe the way in which external factors may affect the rate of photosynthesis.

50. What do you understand by guttation? Under what conditions does it occur?

51. Give an account of the process of photosynthesis.

52. Write brief illustrated notes on the structural peculiarities exhibited by Xerophytes.

53. Give an account of the water relations of a plant cell.

54. Describe briefly the way in which the stomata may regulate the rate of transpiration.

55. Write a short essay on the " Transpiration stream."

56. Mention three insectivorous plants, and describe the structures that are adapted for catching or trapping the animals in each case.

57. Describe the characters of any flowering plants with which you are familiar, that are total parasites or total saprophytes.

58. What is phototropism? How would you account for the phenomena presented? Give examples to indicate the biological significance of phototropism.

59. What is meant by irritability as applied to plants? Illustrate your answer by reference to growing stems and roots.

60. Describe two examples of twining plants. How is twining effected?

61. What is meant by geotropism? Write an account of any three experiments you may have performed in order to investigate the nature of geotropic phenomena in roots.

62. Give an account of the growth, structure, and function of tendrils.

63. Describe carefully how you would fit up an experiment which would show clearly the effect of light on the direction of growth of the stem of a seedling. State briefly the *other* effects of light on plants.

64. Mention some leaves which show movements. Have these movements any biological significance?

65. Write a short essay on Nastic movements.

66. Give an explanatory account of the phototropic and geotropic curvatures shown by the coleoptile of *Avena*.

67. When a dicotyledonous plant is placed in a horizontal position the stem near the apex soon bends until it occupies a vertical position. What explanations have been put forward to account for this bending?

68. Give an account of the effects of light on plants.

69. Mention six plant enzymes and state the reactions that they catalyse. Give a short account of the properties of enzymes.

70. What do you understand by the term "correlation" as applied to plants?

71. Examine and draw the flowers of any five of the following: pea (*Pisum*), foxglove (*Digitalis*), buckwheat (*Fagopyrum*), *Portulaca*, mustard, orange (or other *Citrus*), *Aconitum*, *Cuscuta*, cinnamon (*Cinnamomum*), apricot (*Prunus*).

72. Give an illustrated description of the structure of an anatropous ovule at the time of fertilisation.

73. Describe, with examples, the structure of (1) a hypogynous, (2) a perigynous, (3) a epigynous flower.

74. What is meant by placentation? Examine and draw the ovary and show the placentation in *Phaseolus*, orange, orchid, *Portulaca*, clove (*Eugenia*), *Ardisia*, *Solanum*.

75. Examine, and make drawings of, the stamens of the foxglove, potato, and a lily, to show (*a*) general form, (*b*) insertion of anthers, (*c*) mode of dehiscence, (*d*) internal structure.

76. In what respects does a flower (*a*) resemble, (*b*) differ from, a vegetative shoot?

77. Give diagrams, with brief descriptions, showing the variation in the form of the ovary and receptacle in the Rosaceae. Give examples of each type.

78. Describe the inflorescences of the following plants: *Aconitum* (monkshood), *Mentha*, *Antirrhinum*, sunflower (*Helianthus*), *Euphorbia*, *Ficus*, *Colocasia*.

79. Briefly describe, with examples, the following forms of inflorescence, and point out the relationship which exists between them: panicle, raceme, umbel, spike, spadix, capitulum.

80. Give a concise summary of various contrivances favouring the cross-pollination of flowers.

81. Give an account of the structure and function of a pollen-grain.

82. Describe the processes which lead to the development of an ovule into a seed.

83. What flowers have you yourself observed being visited by wasps, by butterflies, by bees?

84. Draw a series of diagrams representing successive stages in the development of a dicotyledonous embryo from the fertilised egg-cell.

85. What are cleistogamous flowers? Name three plants in which they are found. What is their significance?

86. How is the endosperm tissue of seeds formed? What is the difference between endosperm and perisperm?

87. What is "double fertilisation"? What is its probable significance?

88. What is a fruit? Describe the following fruits: strawberry, raspberry, apple, mango, lichi and orange. What is the nature of the edible portion in each case?

89. Write a short account of the structure of the more common dry, dehiscent fruits, and explain how the seeds are dispersed in those examples you select.

90. Give instances of seeds or fruits which are dispersed (*a*) through the agency of the wind, and (*b*) through the agency of animals. Of what advantage is it to plants that their seeds should be thus dispersed?

91. Describe and compare the fruits of the rose, fig, blackberry, and mulberry.

92. Describe examples of explosive fruits, and try to explain the mechanism in each case.

93. Write a short essay on the dispersal of seeds and fruits by animals, and indicate any special structures in the seed or fruit which ensure such dispersal.

94. Describe the flowers of larkspur and monkshood, and compare them with a *Ranunculus* flower.

95. Write an account of the floral structure and the methods of pollination met with in Cruciferae.

96. Describe the flowers of *Mentha*, *Salvia* and *Ocimum*.

97. How are all Scrophulariaceae distinguished from all Labiatae? Mention plants in both families which might at first sight be confused.

98. Describe how pollination is effected in various members of the family Campanulaceae, and compare it with the method of pollination in Compositae.

99. Name the orders to which the following plants belong and indicate briefly why you refer them to these orders: *Agave*, *Aloe*, *Opuntia*, *Ricinus*, *Phoenix*, *Lagenaria*, *Cuscuta*, *Striga*, *Gossypium*, sweet potato (*Ipomoea*), *Solanum* (potato).

100. Compare the flower of (*a*) an orchid, (*b*) a grass, with that of a lily.

101. Describe the mechanism of pollination in *Striga*, sage, *Antirrhinum*, and *Mimulus*.

102. Describe the flower and method of pollination in a named member of the Papilionatae.

103. Give a general sketch of the life history of a fern from the germination of the spore to the formation of the fertile frond.

104. Give an account of the structure and function of the prothallus of a fern.

105. Indicate the more important structural differences between the sporophyte and gametophyte generations in the fern. How would you account for these differences?

106. What is meant by an "alternation of generations" in the life history of a plant? Illustrate your answer by reference to the life history of a fern.

107. Indicate the more important differences between the fern and *Selaginella*.

108. In what important respects does the life history of a Vascular Cryptogam (*a*) resemble, (*b*) differ from, that of a Flowering Plant? What is the significance of these resemblances and differences?

109. Give a comparative account of the nourishment of the embryo in Vascular Cryptogams and Flowering Plants.

110. Give a comparative account of the development of sporangia and spores in the fern, *Equisetum* and *Selaginella*.

111. Compare the vascular system in the stem of the male fern with that of the stem of the sunflower.

112. Compare the development of the ovule in the Angiosperm with that of the megasporangium in *Selaginella*.

113. Point out clearly the resemblances and differences between *Selaginella* and an *Angiosperm* as regards (*a*) the gametophyte generation, (*b*) the process of fertilisation.

114. Describe in detail the structure of the stem in *Pinus* or *Taxus* after three years of secondary thickening. Explain how the growth in thickness takes place.

115. Describe the structure of the mature ovule of a Gymnosperm and point out the differences between it and the mature ovule of an Angiosperm.

116. What is a gametophyte? Give an account of the gametophyte of *Pinus* or *Taxus*.

117. What are the resemblances and what the differences between the floral organs of an Angiosperm and those of *Pinus* or *Taxus?*

118. Compare the processes of pollination and fertilisation in *Cycas*, *Pinus* (or *Taxus*), and an Angiosperm.

119. In what respects do the reproductive organs of *Taxus* differ from those of *Cycas?*

120. Describe the general external characters of a cycad, and state the more important resemblances to the fern.

121. Compare the development of the megaspore in *Pinus* or other Gymnosperm and a Flowering Plant.

122. Describe the reproductive processes of *Pinus* and *Equisetum*.

123. How are the spores of a fern liberated?

124. Make labelled drawings to show the structure of both micro- and mega-sporophylls, and sporangia of *Pinus* or *Taxus* and of the corresponding structures of an Angiosperm.

125. What is a seed? How does it differ from a spore?

126. Give an account of the structure and life history of *Pellia*.

127. State clearly the grounds on which the conclusion is based that the moss-plant corresponds to the prothallus of the fern, and the sporogonium to the fern-plant.

128. Describe and compare the structure of the thallus as found in *Vaucheria*, *Spirogyra*, *Ulothrix*, *Oedogonium*, and *Fucus*.

129. Give an account of the structure and life history of *Vaucheria*, and indicate the more important resemblances and differences presented in the structure and life history of *Pythium*.

130. Give a full account of the differences which exist between an Alga and a Fungus with regard to the mode of their nutrition.

131. Give a comparative account of sexual reproduction as found in *Chlamydomonas*, *Spirogyra*, *Fucus*, *Pellia*, and an Angiosperm.

132. Describe the normal vegetative condition of *Chlamydomonas*, and compare it with that of *Pleurococcus*.

133. Compare and contrast *Eurotium* and *Spirogyra* as regards their nutrition and reproduction.

134. Describe the structure and life history of the yeast plant. Mention the points in which this plant resembles and differs from *Eurotium* or *Penicillium*.

135. Describe and contrast the development of asexual reproductive cells in *Ulothrix*, *Oedogonium*, *Vaucheria*, *Pythium*, *Eurotium*, and *Funaria*.

136. What is fermentation ? What is its probable significance in relation to the normal metabolic processes ?

137. Is it possible to grow a Mould and Flowering Plant in artificially prepared aqueous solutions ? State what should be the ingredients of such solutions, and explain in what important respect they must differ in the two cases.

138. Name and illustrate by reference to particular types the various modes of reproduction found in plants.

139. What is a parasite ? Give examples. How is a parasite distinguished from (*a*) an epiphyte, (*b*) a saprophyte ? Give examples of epiphytes and saprophytes.

140. Write a short essay on " The Physiology of Bacteria."

141. Give an account of the processes of nitrification and nitrogen fixation. Mention the biological significance of these processes.

142. What is symbiosis ? Describe clearly one example of symbiosis with which you are familiar.

143. Give an account of the structure and life history of a rust fungus.

144. Write brief notes on any three Fungi that cause plant diseases.

145. Name six plants that live wholly or partially submerged in water, and give an account of the structure of any one of them.

146. Describe some experiments of Mendel's with which you are familiar.

147. What are mutations ? How may they arise and what is their significance ?

148. Mention the more important contributions made to our knowledge of genetics and evolution by Lamarck, Mendel, de Vries, and Darwin.

149. Why are plants not always exactly like their parents ?

150. Write brief notes on allelomorphs, crossing over, linkage, and lethal factors.

151. To what extent does our knowledge of the behaviour of the nucleus at meiosis help to explain the results of Mendel's experiments ?

152. Describe and explain the Mendelian inheritance of one pair of contrasted characters.

153. When a tomato plant with red fruits and smooth stems is crossed with another variety having yellow fruits and hairy stems all the progeny (F_1) have red fruits and hairy stems. How do you explain this ? Forecast the results, giving reasons, from " selfing " the F_1 plants.

154. If a tall pea plant bearing red flowers is crossed with a dwarf one bearing white flowers the progeny (F_1) are all tall with red flowers. Explain this result and state, with reasons, the expectations from crossing one of these F_1 plants with the dwarf, white flowered parent.

155. How would you proceed to propagate a hybrid plant ?

156. Give an account of the various soil factors that may affect the distribution of plants.

157. Discuss the conditions prevailing either in a tropical rain-forest or in a " dry " evergreen forest.

158. What are the environmental conditions governing mangrove swamps ? Name the chief genera that are represented in mangrove vegetation.

159. What special features are possessed by mangroves that enable them to thrive in their special habitats ?

160. What are the ecological factors involved in the development of salt marsh ?

161. Give an account of the vegetation of beach-jungle.

162. Describe the environmental factors which operate in the building up of sand-dunes.

INDEX OF VERNACULAR NAMES

ACH, *Morinda citrifolia.*
Adalsa, *Adhatoda Vasica.*
Adambu, *Ipomoea biloba*, Goat's Foot.
Adipalem, *Myristica fragrans*, Nutmeg.
Adrak, *Zingiber officinale*, Ginger.
Aga-mula-neti-wel, *Cuscuta chinensis*, Dodder.
Agast, *Sesbania grandiflora.*
Ahu = Ach.
Ak, *Calotropis gigantea* and *C. procera.*
Akanda = Ak.
Akáshbel, *Cuscuta reflexa*, Dodder.
Aker-tuba, *Derris* (root).
Akhrot, *Juglans regia*, Walnut.
Akkinichilam, *Gloriosa superba.*
Al = Ach.
Ala, *Ficus benghalensis*, Banyan.
Alagai, *Agave.*
Alangai, *Ipomoea Bona-nox*, Moonflower.
Alari, *Nerium oleander*, Oleander.
Alariya, *Plumeria acutifolia*, Templetree.
Alash, *Cassia fistula*, Indian Laburnum.
Ali = Ala.
Alkushi = Akáshbel.
Alla = Adrak.
Alsí, *Linum usitatissimum*, Flax.
Alú, *Solanum tuberosum*, Potato.
Alú bukhárá, *Prunus* sp.
Alúchá, *Prunus communis.*
Am = Amba, *Mangifera indica*, Mango.
Amaltás = Alash.
Amandam, *Ricinus communis*, Castor-oil Plant.
Ambli = Amlá, *Phyllanthus Emblica.*
Amlí, *Tamarindus indica*, Tamarind.
Amliká = Ambli.
Amlok, *Prunus lanata.*
Amrúd, *Psidium Guyava*, Guava.
Amudala = Amandam.
Anár, *Punica granatum*, Pomegranate.
Anantamul, *Hemidesmus indicus*, Indian sarsaparilla.
Anasa, *Ananas sativus*, Pineapple.
Anekattali = Alagai.
Angúr, *Vitis vinifera*, Grape Vine.
Anjír, *Ficus carica*, Fig.
Anoda, *Abutilon indicum.*
Annasi = Anasa.
Aparajita, *Clitoria Ternatea*, Musselshell Creeper.
Aracu, *Ficus religiosa*, Bo-tree, Sacred Peepul.
Arahar, *Cajanus indicus*, Pigeon-pea.
Arale, *Gossypium herbaceum*, Cotton Plant.
Araliya = Alari.
Aranda = Amandam.
Arasu = Aracu.
Arati, *Musa paradisiaca*, Plantain.
Arayal = Aracu.
Ardapal = Alú.
Arhon, *Brassica juncea.*
Ari, *Oryza sativa*, Rice, Paddy.
Arjuna, *Terminalia Arjuna.*
Arú, *Prunus persica*, Peach.
Asan, *Eruca sativa*, Rocket.
Ashok, *Saraca indica.*
Atá, *Anona squamosa*, Custard Apple of India.
Atashi, *Crotalaria sericea*, Rattlewort.
Atipich, *Helianthus tuberosus*, Jerusalem Artichoke.
Audla = Amandam.
Avodala = Amandam.

BABÚL, *Acacia arabica*, Gum-tree.
Baccangayi, *Citrullus vulgaris*, Watermelon.
Bachata, *Urena.*
Bádám, *Prunus amygdalus*, Almond.
Badanike, *Loranthus.*
Badaram, *Zizyphus Jujuba*, Jujube.
Badu-irungu, *Zea Mays*, Maize.
Bael, *Aegle Marmelos*, Wood-apple.
Bagnai, *Capparis horrida*, Caper.
Baherá, *Terminalia Chebula*, Myrobalan (fruits).
Baini, *Corypha umbraculifera*, Talipot Palm.
Baingan, *Solanum Melongena*, Eggplant.
Bájrá, *Pennisetum typhoideum*, Pearl or Bulrush Millet.
Baklá, *Vicia faba*, Broad Bean.
Bakul, *Mimusops Elengi.*
Bale = Arati.
Bán, *Quercus*, Oak.
Ban-chal, *Desmodium gyrans*, Telegraph Plant.

Bandakka, *Hibiscus esculentus*, Lady's Finger.
Bandura-wel, *Nepenthes*, Pitcher-plant.
Ban-kapas, *Hibiscus vitifolius*.
Ban-kapásí, *Thespesia populnea*, "Tulip-tree."
Bankhor, *Aesculus indica*, Indian Horse-chestnut.
Ban-jam, *Eugenia fruticosa*.
Ban-okra = Bachata.
Ban-matar, *Lathyrus aphaca*.
Bans, *Dendrocalamus strictus*, Bamboo.
Bar = Ala.
Bara-shim, *Canavalia ensiformis*, Sword Bean.
Barbati, *Vigna Catiana*, Asparagus Bean.
Baringû, *Caltha palustris*, Marsh Marigold, King-cup.
Basak = Adalsa.
Batala, *Ipomoea Batatas*, Sweet Potato.
Bataun = Baingan.
Bat-baran, *Euphorbia antiquorum*.
Bed, *Salix tetrasperma*, Willow.
Bedatige = Adambu.
Bed-i-Majnún, *Salix babylonica*, Weeping Willow.
Bel = Bael.
Bela, *Feronia elephantum*, Elephant Apple.
Belipatta, *Hibiscus tiliaceus*.
Bena, *Andropogon squarrosus* (= *A. muricatus*).
Ber = Badaram.
Berela, *Sida cordifolia*.
Bet, *Calamus tenuis*, Cane.
Bette, *Areca Catechu*, Areca-nut.
Bhang, *Cannabis sativa*, Hemp.
Bhatta = Ari.
Bhekar = Adalsa.
Bhiláwá, *Semecarpus Anacardium*, Marking Nut.
Bhindi = Bandakka.
Bhojpatra, *Betula bhojpatra* = *B. utilis*, Birch.
Bhurj = Bhojpatra.
Bhuttá = Badu-irungu.
Bichhú bútí, *Girardinia heterophylla*.
Biduru, *Bambusa*, Bamboo.
Bihi, *Cydonia vulgaris*, Quince.
Bilejola, *Sorghum vulgare*, Millet, Guinea-corn.
Bil-rai, *Nasturtium indicum*.
Binafshá, *Viola*.
Boch, *Acorus Calamus*, Sweet Flag.
Bo-gaha = Aracu.
Bor = Badaram.
Brinjal = Baingan.
Bu-dada-kiriya, *Euphorbia hirta*.
Bulat-wel, *Piper Betle*, Betel.
Buroni, *Ficus pumila*, Ceylon Ivy.
Butsarana, *Canna indica*, Canna.

CAGIDA, *Camellia Thea*, Tea.
Cakka, *Artocarpus integrifolia*, Jak.
Callejadda, *Asparagus racemosus*.
Camangai, *Mimosa pudica*, Sensitive-plant.
Caronda, *Carissa Carandas*.
Cavala, *Cycas*.
Cayccadi = Cagida.
Chachindá, *Trichosanthes anguina*, Snake-gourd.
Chái = Cagida.
Chakotrá, *Citrus decumana*, Pomelo, Shaddock.
Chakunda, *Beta vulgaris*, Beetroot.
Chaltá, *Dillenia indica*.
Chambá, *Michelia Champaka*.
Chambeli, *Jasminum*, Jasmine.
Chamelí = Chambeli.
Champak = Chambá.
Chaná, *Cicer arietinum*, Chick-pea, Gram.
Chándaní, *Tabernaemontana coronaria*.
Chandrakanti = Alangai.
Chandramallika, *Chrysanthemum*.
Charas = Bhang.
Chattavari = Callejadda.
Chával = Ari.
Chavukkai, *Casuarina*.
Cheena, *Panicum miliaceum*, Indian Millet.
Cheraku, *Saccharum officinarum*, Sugar-cane.
Chhagal-bat, *Naravelia*.
Chhatim = Chhatium, *Alstonia scholaris*, Devil-tree.
Chhota dhatura, *Xanthium Strumarium*, Cockle-bur.
Chichinda = Chichinga = Chachinda.
Chíl, *Pinus longifolia*.
Chilghoza, *Pinus Gerardiana*, Gerard's Pine.
China-badam, *Arachis hypgœa*, Ground Nut.
Chínár, *Platanus orientalis*, Plane.
Chinta = Amlí.
Chír = Chíl.
Chirátá, *Swertia Chirata*, Chiretta.
Chirru = Chhota-dhatura.
Cholam = Badu-irungu.
Chorkanta, *Andropogon aciculatus*, Love-thorn.
Cita = Ata.

Cocam, *Cocos nucifera*, Coconut Palm.
Col = Chavukkai.
Colam = Bilejola.
Croton, *Croton Tiglium*.
Cunthi = Adrak.

DADIMA = Anár.
Dakhanga, *Delphinium coeruleum*, Larkspur.
Dálchíní, *Cinnamomum zeylanicum*, Cinnamon.
Daluk = Bar-baran.
Damala, *Phaseolus lunatus*, Lima Bean.
Dasala, *Hibiscus rosa-sinensis*, Shoe-flower, China Rose.
Dasavana = Dasala.
Datúrá, *Datura Stramonium*, Thorn-apple.
Dekani-babul, *Pithecolobium dulce*.
Delum = Anár.
Deodár, *Cedrus deodara*, Himalayan Cedar.
Dhák, *Butea frondosa*, Parrot-tree, Flame of the Forest.
Dhaincha, *Sesbania cannabina*.
Dhán = Ari.
Dhania, *Coriandrum sativum*, Coriander.
Dhátrí, *Woodfordia floribunda*.
Dhatúrá = Datura.
Dheras = Bandakka.
Dhundul, *Luffa ægyptica*, Loofah, Bath-sponge.
Dhutra, *Datura fastuosa*.
Diár = Deodar.
Diwul = Bela.
Diyalabu, *Lagenaria vulgaris*, Bottle Gourd.
Dodan, *Citrus Aurantium*, Orange.
Dodanimbe, *Citrus Limonia*, Lemon.
Drek, *Melia Azedarach*, Persian Lilac.
Durba-ghas, *Cynodon dactylon*, Dog's-tooth, Bermuda grass.

ERAPILLAKAI, *Artocarpus incisa*, Bread Fruit.

FÁLSÁ, *Grewia asiatica*.

GAB-NAL, *Arundo Donax*.
Gagla = Ban-matar.
Gájar, *Daucus carota*, Carrot.
Galgal, *Citrus medica*, Citron.
Galis, *Gardenia latifolia*.
Gam-miris-well, *Piper nigrum*, Pepper.
Gandapana, *Lantana*.
Gándhelá, *Murraya Kœnigii*, Curry Leaf.
Gánjá, *Cannabis sativa*, Hemp.
Ganná = Cheraku.
Gaurí-phal, *Rubus*, Bramble.
Geru, *Anacardium occidentale*, Cashew-nut.
Ghiya = Diyalabu.
Ghiya-tori = Dhundul.
Gila = Gilatije, *Entada scandens*.
Ginpol, *Nipa fruticans*.
Gobhi, *Elephantopus scaber*.
Godduyishalu = Cavala.
Godhumalu = Godumai = Gom, *Triticum vulgare*, Wheat.
Golap-jam = Gulab-jamin = *Eugenia Jambos*, Rose-apple.
Gonduli, *Panicum miliare*, Little Millet.
Gram = Chaná.
Guláb, *Rosa indica*, Rose.
Gul-achin = Alariya.
Gulaganji, *Abrus precatorius*, Indian Liquorice, Crab's-eyes.
Gúlar, *Ficus glomerata*.
Guliajaib, *Hibiscus mutabilis*.
Gul-i-dáúdi = Chandramallika.
Gul-khairá, *Althaea rosea*, Hollyhock.
Gulmohr, *Poinciana regia*, Gold Mohur Tree, Flamboyante.
Gunja = Gulaganji.
Gurki, *Solanum nigrum*, Black Nightshade.
Gurgunji = Gulaganji.

HALDÍ, *Curcuma longa*, Turmeric.
Halencha, *Enhydra fruticans*, Indian Watercress.
Hálim = Halim-sak = Halon, *Lepidium sativum*, Garden Cress.
Haralu = Amandam.
Hargoza = Harkuchkanta, *Acanthus ilicifolius*.
Harir = Baherá.
Harmal, *Peganum Harmala*.
Hashish = Bhang.
Has-na-hana, *Cestrum*, Queen of the Night.
Hatichoke = Atipich.
Hatti, *Bombax malabaricum*, Red Cotton Tree.
Heen-dan, *Eugenia corymbosa*.
Heen-gendakola, *Portulaca oleracea*.
Henná, *Lawsonia inermis*.
Hing, *Ferula foetida*, Asafoetida.
Hire, *Luffa acutangula*, Ribbed-gourd.
Hottutirugana, *Helianthus annuus*, Sunflower.
Huliyugura = Akkinichilam.

IKILI = Hargoza.
Illi = Biduru.
Imli = Amlí.
Inci = Adrak.
Indi, *Phoenix zeylanica.*
Indrayan, *Citrullus Colocynthis*, Colocynth, Bitter Apple.
Indu, *Caryota urens.*
Inguru = Adrak.
Irulli, *Allium Cepa*, Onion.
Ispagúl, *Plantago ovata*, Ispagula.
Itta, *Phoenix dactylifera*, Date Palm.

JABA = Dasala.
Jaiphal = Adipalem.
Jaji = Adipalem.
Jal-khumbi, *Pistia Stratiotes*, Water-lettuce.
Jama = Amrud.
Jamalgota = Jaypal = Croton.
Jáman = Jambú.
Jamaphala = Jama.
Jambú = Golap-jam.
Jand, *Prosopis spicigera.*
Jangliám, *Spondias mangifera.*
Japa = Dasala.
Jarrah, *Eucalyptus marginata.*
Jasum = Dasala.
Jata-mansa, *Balanophora.*
Jatikka = Adipalem.
Jhinga = Hire.
Job, *Hordeum vulgare*, Barley.
Juar = Bilejola.
Judwâr, *Delphinium denudatum*, Larkspur.

KABAS = Arale.
Kabbu = Bilejola.
Kachálú = Kachu, *Colocasia antiquorum*, Tara, Tania.
Kachnár, *Bauhinia variegata*, Mountain Ebony.
Kadam, *Nauclea Cadamba* = *Anthocephalus indicus.*
Kaddu = Diyalabu; also *Cucurbita Pepo*, Vegetable Marrow, Pumpkin.
Kadol, *Rhizophora mucronata*, Mangrove.
Káfúr, *Cinnamomum Camphora*, Camphor.
Kagji-Nebu, *Citrus medica* var. *acida*, Sour Lime.
Kahir, *Lactuca sativa*, lettuce.
Kail, *Pinus excelsa*, Bhotan Pine.
Kaivalli, *Dioscorea*, Yam.
Kájú = Geru.
Kala-jira, *Nigella sativa*, Devil-in-a-Bush, Love-in-a-Mist.
Kala-kunch, *Coix lachryma-jobi*, Job's Tears.
Kalinga = Chaltá.
Kali-tori = Hire.
Kallangadi = Baccangayi.
Kalmi-sak, *Ipomoea reptans.*
Kalnaru = Alagai.
Kaluwara, *Diospiros Ebenum*, Ebony.
Kamád = Bilejola.
Kamal, *Nelumbium speciosum*, Lotus.
Kamala, *Mallotus philippinensis.*
Kamappu = Cavala.
Kambil = Galis.
Kambu, *Bambusa.*
Kamrakh = Kamrang, *Averrhoa Carambola.*
Kanchan = Kachnar.
Kandal = Akkinichilam.
Kandamani = Butsarana.
Kandol = Kadol.
Kaner = Alari.
Kankum, *Ipomoea aquatica.*
Kantala = Alagai.
Kanval, *Nymphaea Lotus.*
Kapás = Arale.
Kapi = Kappi, *Coffea arabica*, Coffee.
Karala, *Momordica Charantia*, Bitter Gourd.
Karal-iringu = Bilejola.
Karélá = Karala.
Kariari = Akkinichilam.
Karil, *Capparis aphylla.*
Karír = Karil.
Karondá = Karanja = Karaunda, *Carissa carandas.*
Karukali = Kaluwara.
Kasa-gaha = Chavukkai.
Kash, *Saccharum spontaneum.*
Kat-bish, *Aconitum.*
Kath-bel = Bela.
Kathá, *Acacia Catechu*, Cutch.
Kattu-ikili = Ikili.
Katu-anoda, *Anona muricata*, Sour-sop.
Katu-imbul = Hatti.
Katu-pathok, *Opuntia Dillenii*, Prickly Pear.
Katu-una = Biduru.
Kaun, *Setaria italica*, Italian Millet.
Kawanch, *Mucuna pruriens*, Cowage.
Kehel = Arati.
Kesar, *Crocus sativus*, Saffron.
Keshuti, *Eclipta alba.*
Kesu = Kachálú.
Khair = Kathá.
Khajúr = Itta.
Khanor = Bankhor.
Kharata, *Dodonaea viscosa.*
Kharbúzá = Kharmuza, *Cucumis Melo*, Melon.

Khas-khas = Khus-khus = Bena.
Khattíbútí, *Oxalis*, Wood Sorrel.
Khesari, *Lathyrus sativus*.
Khírá, *Cucumis sativus*, Cucumber.
Khirak, *Celtis australis*.
Kikar = Babúl.
Kiribadu, *Ipomoea digitata*.
Kittale = Dodan.
Kittanara = Alagai.
Kitul = Indu.
Kobbari, *Cocos nucifera*, Coconut Palm.
Korkochi, *Capsicum grossum*, Chillies.
Kopee = Kapi.
Kos = Cakka.
Kotampan = Godhumalu.
Krishnatamara = Butsarana.
Krishnachura = Gulmohr.
Kuchla, *Strychnos Nux-vomica*, Nux-vomica.
Kukar-songa, *Blumea lacera*.
Kukshim, *Vernonia cinerea*.
Kulhárí = Akkinichilam.
Kumoi, *Careya arborea*, Patana Oak.
Kumra, *Cucurbita Pepo*, Vegetable Marrow, Pumpkin (also = Diyalabu).
Kunch = Kundumani = Kunnikkuru = Gulaganji.
Kuntala = Heen-dan.
Kuntineradu, *Eugenia bracteata*.
Kuppamani, *Acalypha indica*.
Kuravan = Itta.
Kuruvichai = Badanike.
Kusam = Kusum = Kushum-phul, *Carthamus tinctorius*, Safflower.
Kusurijang, *Mentha viridis*, Mint.
Kuturi, *Lupinus*, Lupin.
Kuvalam = Bael.

LAI-SAK, *Brassica rugosa*.
Lajjabati-lata = Lajwanti = Camangai.
Lakuch, *Artocarpus Lakoucha*.
Lál chandan, *Pterocarpus santalinus*.
Lál mirch, *Capsicum annuum*, Chillies, Red Pepper.
Languli-lata, *Ipomoea Pes-tigridis*.
Lassan, *Allium sativum*, Garlic.
Lasúrá, *Cordia myxa*.
Lau = Diyalabu.
Lavang, *Eugenia caryophyllata*, Clove.
Lichí, *Litchi chinensis*, Litchi.
Límú = Dodanimbe.
Longan, *Nephelium longana*.
Louná, *Anona reticulata*, Bullock's Heart, Custard-apple of W. Indies.

MA = Am.
Madár = Ak.
Madugaha = Cavala.
Madulam = Anár.
Maha-dan, *Eugenia jambolana*.
Maha-nuga = Ala.
Mahwa, *Bassia latifolia*.
Maindí = Henná.
Majnún = Bed-i-Majnún.
Makaí = Badu-irungu.
Makna, *Euryale ferox*.
Malainavia = Kuntala.
Malu-miris = Korkochi.
Mamiri = Baringu.
Mamphal = Katu-anoda.
Mancanarri = Ach.
Mandar, *Erythrina indica*, Coral Tree.
Mandavalli = Alangai.
Manduá = Marhua, *Eleusine coracana*, Millet, Kurakkan, Ragi.
Mangai = Biduru.
Mani = Ala.
Manioca = Man-iokka, *Manihot utilissima*, Manioc, Tapioca.
Manjeeth, *Rubia cordifolia*.
Mankachu, *Alocasia indica*.
Maranda, *Eugenia spicata*.
Mareda = Bel.
Maricetu = Ala.
Marungi = Maranda.
Másh, *Phaseolus radiatus*, Black Gram.
Masúr, *Lens esculenta*, Lentil.
Matalam = Límú.
Matar, *Pisum sativum*, Pea.
Mavidi = Mavu = Am.
Mekkejola = Badu-irungu.
Mesta, *Hibiscus Sabdariffa*, Roselle.
Methí, *Trigonella Foenum-graecum*, Fenugreek.
Mhár = Kitul.
Míthá álú = Batala.
Milaku = Gam-miris-well.
Minchi = Kusurijang.
Mitha-aloo = Batala.
Mitha-kumra, *Cucurbita maxima*, Sweet Gourd, Squash-gourd or Pumpkin.
Moong, *Phaseolus Mungo*.
Motabi = Chakotra.
Moth, *Phaseolus aconifolius*.
Mudár = Ak.
Muda-bin-tanburu = Adambu.
Múlá = Muli, *Raphanus sativus*, Radish.
Mullilavu = Hatti.
Mulluvellarika = Khira.
Múng = Másh.
Múng phali = China-badam.
Mûnila = Judwâr.
Munthirikai = Geru.

NACIKEGIDA = Camangai.
Nagaramukthi = Alangai.
Nág-phana = Katu-pathock.
Nal, *Phragmites karka*, Reed.
Nali = Kalmi-sak.
Namaraivalai = Arati.
Naran = Dodanimbe.
Nárangí = Dodan.
Naranna = Nárangí.
Náryal = Cocam.
Náspátí, *Pyrus communis*, Pear.
Naval peru = Maha-dan.
Nebu = Dodanimbe.
Nelakadalai = China-badam.
Nellu = Ari.
Nelu, *Strobilanthes amabilis*.
Nelun = Kamal.
Neoza = Chilghoza.
Neruda = Maha-dan.
Níl, *Indigofera tinctoria*, Indigo Plant.
Nil-lata, *Thunbergia grandiflora*.
Nilofar, *Nymphaea alba*, Water-lily.
Nil-padma, *Nymphaea stellata*.
Ním, *Azadirachta indica*.
Nimbu = Dodanimbe.
Nímú = Límú.
Nirbisi = Judwâr.
Nirulli = Irulli.
Niyangala = Akkinichilam.
Noná = Louná.

OGAL = Ogalá, *Fagopyrum esculentum*, Buckwheat.
Oka = Caronda.
Ol-kopi = Kohl-rabi (*Brassica oleracea*).
Olinda-vel = Gulanji.
Olu = Nilofar.

PADMA = Kamal.
Pakka = Pakku = Bette.
Palacu = Cakka.
Palas = Dhak.
Pallavi = Bu-dada-kiriya.
Palwal, *Trichosanthes dioica*.
Pán = Bulat-wel.
Pana = Jal-khundi.
Panasa = Cakka.
Panei = Arale.
Papayá = Pappayi, *Carica Papaya*, Papaw.
Paras = Ban-kapásí.
Patola = Chachindá.
Patti = Arale.
Pepol = Papayá.
Peral = Ala.
Petan = Kachnár.
Petari = Anoda.
Phálsá = Fálsá.
Pháphar, *Fagopyrum tataricum*.
Phuti = Kharbúzá.
Piáz = Irulli.
Pilakai = Cakka.
Pilila = Badanike.
Pinjari, *Thalictrum*.
Pipal = Aracu.
Pipini = Khira.
Pirku = Hire.
Pissu-már, *Bœnninghausenia albiflora*.
Pistá, *Pistacia vera*, Pistachio-nut.
Podíná = Kusurijang.
Poduk, *Pterocarpus dalbergioides*, Andaman Red-wood.
Pol = Cocam.
Post, *Papaver somniferum*, Opium Poppy.
Pudíná = Podíná.
Pulás = Dhak.
Puli = Amlí.
Pulluni = Badanike.
Puwak = Bette.

QAHVA = Kapi.
Quash, *Sechium edule*, Squash.

RABU = Mulá.
Ragi = Manduá.
Rai = *Brassica Napus*.
Rakto-Kambal, *Nymphaea rubra*.
Rambutan, *Nephelium lappaceum*.
Rám-phal = Louná.
Ramsita = Louná.
Ras-bhari, *Physalis peruviana*, Cape Gooseberry.
Rata-del = Erapillakai.
Ratakaju = China-badam.
Ratak = Rati = Gulaganji.
Rattam, *Dracaena*.
Ravi = Aracu.
Regu = Badaram.
Rehri = Amandam.
Ríthá, *Sapindus Mukorossi* and *S. laurifolius*, Soap-nut.
Rudráksh, *Elaeocarpus Ganitrus*.
Ruí = Arale.

SA-DIKKA = Adipalem.
Safeda, *Populus*, Poplar.
Safed chandan, *Santalum album*, Sandal-wood.
Sagon = Sagun, *Tectona grandis*, Teak.
Sakarkandi = Batala.
Sál, *Shorea robusta*.

Salád = Kahir.
Samudra-sok, *Argyreia speciosa*, Elephant Climber.
San, *Crotalaria juncea*, Sunn-hemp.
Sanatta = Kharata.
Sandal = Saíed chandan.
Sankukra, *Hibiscus cannabinus*, Madras or Deccan Hemp.
Sánp búti, *Arisaema Wallichianum*, and other spp., Cobra or Snake Plant.
Sárisha = Arhon.
Sarson, *Brassica campestris*, var. *Sarson*.
Sasha = Khira.
Sarv, *Cupressus*, Cypress.
Saryamu, *Gam-miris-well*.
Satamuli = Callejadda.
Saunf, *Fœniculum vulgare*, Fennel.
Seb, *Pyrus Malus*, Apple.
Seetha = Katu-anoda.
Sem, *Dolichos Lablab*, Lablab.
Shaftálú = Arú.
Shakarkandi = Batala.
Shalgam, *Brassica campestris* var. *rapa*, Turnip.
Shálmalí = Hatti.
Shalook = Kanval.
Sharifá = Atta.
Shim = Sem.
Shisham, *Dalbergia Sissoo*.
Shola, *Aeschynomene aspera*.
Shomi = Jand.
Shondal = Alash.
Shone = San.
Shyama, *Panicum crus-galli*.
Siáh mirch = Gam-miris well.
Sigenasu = Batala.
Sikku = Adrak.
Sil-koroi, *Albizzia lucida*.
Simal = Simul = Hatti.
Singhárá, *Trapa bicornis*, and *T. natans*.
Siriphal = Bel.
Sirís, *Albizzia Lebbek*.
Sitá phal = Ata.
Sitsal, *Dalbergia latifolia*, Indian Rosewood.
Soá, *Anethum graveolens*, Dill.
Soánjaná, *Moringa pterigosperma*.
Solá = Shola.
Somlata, *Sarcostemma brevistigma*.
Somraj, *Vernonia anthelmintica*.
Sringavera = Adrak.
Sthalpadma = Guliajaib.
Supárí = Bette. Lagenaria Vulgaris
Suraikkai = Diyalabu.
Suraj-mukhi = Hottutirugana.
Suriya = Ban-kapásí.
Suriya-kanti = Suraj-mukhi.
Swarni-lata = Akáshbel.
Swet-rai = Asán.
Swet-sarisha = Sarson.
Swet-simul, *Eriodendron*, White Cotton Tree.

TAGAR = Chándaní.
Takkali, *Lycopersicum esculentum*, Tomato.
Tál, *Borassus flabellifer*, Palmyra Palm.
Tala = Tara = Baini.
Tali, *Ipomoea hederacea* and *Dalbergia Síssoo*.
Tamarhindí = Amlí.
Tamarira = Asán.
Tambákú, *Nicotiana tabacum*, Tobacco.
Tara = Taro = Baini.
Taranuri = Swet-rai.
Tarbuza = Tarmuz = Baccangayi.
Teagida = Cagida.
Tejbal, *Zanthoxylum alatum*.
Tembiliya = Kuntineradu.
Tena = Cocam.
Tengai = Cocam.
Tey-ile = Cagida.
Thale, *Pandanus odoratissimus*, Screw-pine.
Thamarai = Kamal.
Thay-gas = Cagida.
Thuner, *Taxus baccata*, Yew.
Tikari kalai = Moong.
Til, *Sesamum indicum*, Sesame.
Tirmar = Tejbal.
Togekoddi, *Avena sativa*, Oat.
Torai = Hire.
Torio = Rai.
Tuba merah, *Derris malaccensis*.
Tuba putch, *Derris elliptica*.
Tulsi, *Ocimum sanctum*, Sacred Basil.
Tun, *Cedrela Toona*, Indian Cedarwood.
Tút, *Morus*, mulberry.

UK, *Cheraku*.
Ulu, *Imperata arundinacea*.
Uralakilangu = Alú.
Uru-wi = Ari.
Uvav = Chaltá.

VAKA, *Carissa spinarum*.
Vakul = Bakul.
Vala-valai = Arati.
Vanikkodi, *Vanilla planifolia*, Vanilla Orchid.
Velkelangu = Batala.

Vempadum = Bakl á.
Vendikai = Bandakka.
Venu = Biduru.
Verkadalai = China-badam.
Verrilai = Bulat-wel.
Viláyatí baingan = Takkali.
Vilvam = Bel.

WACH = Boch.
Wara = Ak.
Wars = Kamala.
Welala = Kaivalli.
Wetur essa, *Drosera Burmanni*, Sundew.
We-wel, *Calamus Rotang*, Rattan.
Wi = Ari.

ZÁFRÁN = Kesar.
Zardálú, *Prunus armeniaca*, Apricot.
Zirá, *Cuminum Cyminum*, Cummin " seed."

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